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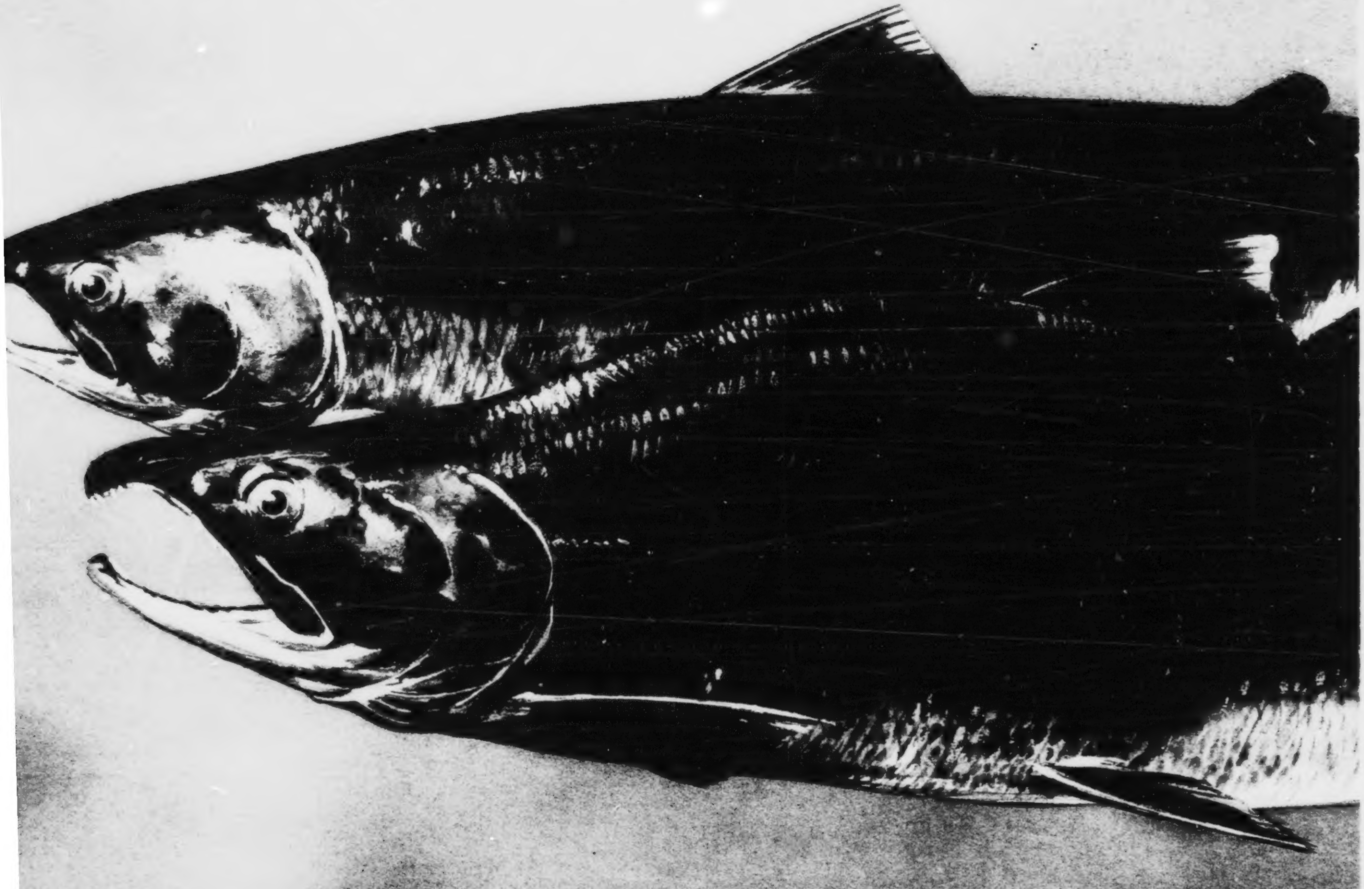
Sockeye Salmon
(Oncorhynchus nerka)
Population Biology and Future Management

Edited by H.D. Smith, L. Margolis, and C.C. Wood



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Sockeye Salmon *(Oncorhynchus nerka)* Population Biology and Future Management

(Proceedings of the
International Sockeye Salmon Symposium — Sockeye '85,
held at Nanaimo, British Columbia, November 19-22, 1985)

Edited by

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Abstract

SMITH, H. D., L. MARGOLIS, AND C. C. WOOD [ED.]. 1987. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 486 p.

A three-day International Symposium on Sockeye Salmon (*Oncorhynchus nerka*) was organized by the Canada Department of Fisheries and Oceans and convened at Nanaimo, British Columbia in November 1985. Advice on subject matter and participation came from an external committee of senior scientists and administrators in contributing agencies in Canada, Japan, the United States, and the Union of Soviet Socialist Republics. The papers included in the proceedings deal with sockeye biology and stock management.

Papers on sockeye biology are divided into those concerned primarily with (a) life history strategies and (b) enhancement and development. Papers dealing with management are divided into (a) the tools of management and (b) management of some principal stocks.

Résumé

SMITH, H.D., L. MARGOLIS, AND C. C. WOOD [ED.]. 1987. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96: 486 p.

Le ministère des Pêches et des Océans du Canada a organisé un Symposium international sur le saumon nerka (*Oncorhynchus nerka*) qui a eu lieu en novembre 1985 à Nanaimo (Colombie-Britannique). Un comité externe composé de scientifiques principaux et d'administrateurs oeuvrant au sein d'organismes participants du Canada, du Japon, des États-Unis et de l'Union des républiques socialistes soviétiques a fourni des conseils sur les questions étudiées. Les études présentées dans le compte rendu portent sur la biologie et la gestion des stocks de saumon nerka.

Les études sur la biologie du saumon nerka sont divisées en deux grandes catégories, soit a) les variantes du cycle vital et b) la mise en valeur et le développement. Dans le cas des études sur la gestion des stocks, elles sont classées en deux groupes, soit a) les outils de gestion et b) la gestion de certains stocks importants.

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Most papers in these proceedings were reviewed by at least two referees. These referees did an outstanding job in identifying the strengths and weaknesses of manuscripts and in recommending some revisions. Their efforts and the response of the authors themselves to the recommendations were, we feel, exemplary. An exception to the rigorous "peer review" was the collection of four Soviet papers. Language limitations and scheduling precluded the same full review of these papers. Our thanks and appreciation are extended to the following people who served as referees for one or more papers: J. Adams, R. Bams, T. Beacham, F. Bernard, T. Bilton, I. Birtwell, D. Blackbourn, R. Burgner, R. Burkett, R. Cook, R. Conrad, R. Cutting, M. Dahlberg, R. Fagen, M. Fredin, M. Fretwell, S. Fried, F. Fukahara, R. Gard, C. Harris, M. Healey, M. Henderson, S. Heizer, K. Hyatt, H. Jaenicke, R. Kadowaki, J. Koenings, R. LeBrasseur, C. Levings, D. Levy, S. Matthews, D. Meerburg, R. Minard, J. McDonald, P. Mundy, M. Nassichuk, D. Noakes, T. Northcote, E. Parkinson, T. Perry, R. Peterman, T. Quinn, W. Ricker, B. Riddell, D. Rogers, W. Saito, D. Shutz, P. Sprout, M. Staley, J. Stockner, R. Straty, R. Thomas, B. Van Alen, C. Walters, C. West, I. Williams, R. Wissmar, J. Woodey, and H. Yuen.

Introduction

Twenty years ago Dr. Earle Foerster of the Pacific Biological Station at Nanaimo, British Columbia, wrote "The Sockeye Salmon". Published in 1968 as Fisheries Research Board of Canada Bulletin No. 162, it is the most comprehensive treatise on sockeye salmon to date. It has served as an invaluable reference in the intervening years and is cited often in the present volume.

More recent research has advanced our knowledge on many aspects of sockeye biology and greatly improved our ability to manage sockeye stocks. But there appears to be a need to consolidate results of these recent studies for both researchers and stock managers to permit ready comparisons of biological events and management practices throughout the range of the species and better determine where and how new precepts could be applied. To encourage this process a 3-day symposium was convened at Nanaimo, British Columbia, in November 1985 with the theme "*Sockeye Population Biology and Future Management*". Thirty-eight papers were invited and a total of 41, including some not presented at the symposium, were subsequently accepted for publication.

Two committees were struck to assist in the development of the symposium and their members and affiliations are recorded above. In addition, three eminent fisheries scientists, Dr. W.E. Johnson of the Canada Department of Fisheries, Professor T.R. Parsons of the Department of Oceanography of the University of British Columbia, and Professor O.A. Mathisen of the Department of Zoology and Fisheries of the University of Alaska at Juneau, Alaska, brought many years of personal sockeye research and management experience to the meeting and effectively moderated discussion in their areas of expertise.

Although a great deal of new information was presented, it was also clear that many fundamental questions of the past remain largely unanswered. Furthermore, sockeye biologists and managers appear divided on the significance of many observations and some of the most attractive generalizations have tended to disintegrate as the biological data series grew. It is hoped that some of the most prominent information gaps will become apparent to readers of the papers in this volume (see for instance Professor Larkin's upbeat address to the gathering).

The symposium was organized under two main subject areas. The first dealt primarily with population biology, including the varied life history strategies of sockeye, and opportunities for enhancing and developing stocks. The second subject area was sockeye stock management. Essential tools of management such as those for improved stock separation and forecasting were discussed and a number of prevailing and proposed management regimes were reviewed.

The first paper, Clifton Forrester's comprehensive review of world distribution and abundance of sockeye salmon both historically and currently, was presented in Forrester's absence by Leo Margolis. Forrester notes that although abundance of combined North American stocks is now comparable with peak historic levels, production of Kamchatkan stocks remains depressed.

Section I: Biology of Sockeye Salmon

a) Life history strategies

Sockeye salmon display the most varied and complex life histories within the genus *Oncorhynchus* and demonstrate a great capacity to adapt to local conditions. For instance, in some populations juvenile sockeye forego the usual period of lake residence, opting for either swift, or staged migrations to salt water as fry or underyearlings. Wood et al., Birtwell et al., and Viktor Bugaev presented new examples of this atypical early life history pattern, which may apply more commonly and in greater variety than we had previously recognized. Both the productive Fraser and Kamchatka rivers produce some of these non-lacustrine types.

Patterns of sockeye movement in their early periods in lakes and in nearshore marine areas may vary considerably. David Levy considers the adaptive value of diel migratory behaviour among lacustrine juvenile sockeye in terms of foraging efficiency in an often hostile environment.

The propensity for freshwater sockeye research projects is seen in the scarcity of detailed new information concerning the months between the seaward and return migrations. Once at sea, juvenile sockeye are presented with a wide range of possible routes to ocean pastures. Yet, as Groot and Cooke inform us, the northerly journey of Fraser River juveniles seems swift, well directed, and often at variance with the pathways used by their parents on their homeward migration. Quinn and terHart offer new evidence from sonar tagged adults of the complex pattern of orientation that accompanies the final approach to natal streams, perhaps bringing us a step closer to understanding that most pervasive and fascinating of the salmon's attributes, the ability to home.

Factors governing age at return remain poorly understood but they are of fundamental importance to sockeye stock management. Donald Rogers observes that for the important Nushagak stock, freshwater age can be shaped by environmental factors, whereas ocean age appears to be largely inherited. However, Peterman and Bradford postulate a non-genetic explanation for correlations in ocean ages of parents and progeny in several Alaskan stocks, invoking an extension of the "maternal effects hypothesis" of Bilton (1971).

Jensen and Mathisen, studying the world's most productive sockeye system, the Kvichak, found that individual spawning grounds drew fish from all major temporal segments of the run. The authors consider this to be an important element in the productivity of the Kvichak stocks. Michael Healey examines variation among life history patterns and compares observed and predicted optimum sizes and ages at maturity.

b) Habitat and development

As human activity encroaches on the habitat of native sockeye populations, the importance of salmon husbandry will grow, and new or improved techniques will be needed to maintain production. This calls for better understanding of the natural phenomena that limit production and of ways to manipulate them to achieve production goals.

Ernest Brannon shows how spawning times and rates of development of ova are adapted to expected temperature regimes, thus assuring a synchrony of fry emergence with forage production cycles in nursery lakes.

Michael Selifonov reports that sockeye recruitment in the streams of the Kurile Lake region of the USSR is related to periodicity in such elements as regional air and water temperatures and water levels. Robert Burgner also attributes patterns of freshwater growth and age of migration to "external" factors such as meteorological conditions, interspecific competition, and predation in Bristol Bay. However, he is convinced that genetic differences also play an important part, citing diverse responses among populations exposed to similar environmental conditions.

O'Neill and Hyatt demonstrate that juvenile sockeye and threespine sticklebacks foraged competitively in enclosure experiments in a Vancouver Island lake. They conclude that when plankton is scarce, these species can modify the plankton community such that both suffer. Such observations have important implications for lake fertilization programs. Jaenicke et al. also studied sympatric sockeye fry and stickleback in Lake Nunavaugaluk in preparation for possible outplants of sockeye fry. They concluded that vegetated shoal areas constitute attractive release sites because they are rich in chironomids and appear favourable for growth and survival.

The role of research in salmon enhancement is well illustrated by the large Babine Lake Development Project discussed by West and Mason. Babine production was limited by available spawning ground until spawning channels were built in the 1970's. Fry and smolt production targets were achieved but adult returns remain below expectations. The experiment has had important implications for enhancement projects in general and continues to provide opportunities for further research. In striking contrast to the extensive Babine project, the simple, low cost Gulkana Streamside Incubation Facility described by Roberson and Holder capitalizes on spring water to achieve an outstanding egg-to-fry success. However, these authors warn us that, like the Babine project, the benefits of significant new production can be reduced by serious new allocation problems for managers.

Industrial fertilizers have been widely used to enrich sockeye lakes. John Stockner and Koenings and Burkett discuss lake trophodynamics in relation to enrichment and note that salmon carcasses are an important factor in the phosphorous cycle. Stockner also comments on energy shunts or "sinks" that may rob juvenile sockeye of the products of lake fertilization. The lake production classification system proposed by Koenings and Burkett based on primary productivity and smolt characteristics offers promise for enhancement planning.

Stock restoration by transplanting has appeal in its directness and relatively low cost, but frequent poor results suggest that much is still to be learned about matching donor stocks to recipient watersheds. Ian Williams recounts three decades of transplant trials on the Upper Adams River and points to some encouraging recent returns.

Parasites can be of considerable interest to salmon stock managers if they harm host populations or can serve as biological tags. Kazuya Nagasawa describes the distribution and prevalence of the common dracunculoid nematode *Philonema oncorhynchi* among sockeye of various ages and maturity stages in the North Pacific Ocean. He concludes that the chief effect of this parasite is simply to cause visceral adhesions, and these are most prevalent in immature fish.

Many sockeye stocks reproduce in waters heavily contaminated with glacial, volcanic, or other particulate matter. Servizi and Martens report that sediments typical of those suspended in the Fraser River killed underyearlings, caused gill trauma in smolts, and evoked stress responses among adults in the laboratory. It seems probable that these deleterious effects could influence the distribution and success of sockeye populations.

Section II: Fishery Management — Past, Present, and Future

a) The tools of management

The best test of research results is their successful application in maintaining healthy and productive stocks generating the greatest possible benefits to users. These applications are usually the task of fishery managers who require close and continued consultation with researchers. The ability to forecast stock abundance is particularly important. Henderson et al. conclude that for the relatively small Smith Inlet sockeye stock, average rate of return and brood year strength are still the most useful predictors of total run size. More sophisticated models using commercial fisheries statistics were less reliable and may be useless in years of severe fishing restrictions. In Alaska, Fried and Yuen report that a simple linear regression model utilizing catch data from the Japanese high seas fishery and Bristol Bay air temperatures gave best results for all Bristol Bay runs combined, whereas models incorporating smolt run data were superior for forecasting the numerically dominant Kvichak runs.

More than 25 years of annual smolt and adult production data exist for the Babine sockeye stocks. Macdonald et al. report that a combination of smolt numbers three years prior, and three-year-olds (jacks) one year prior, to a return gave the best pre-season estimate of both Babine and combined Skeena sockeye stock size. However, such forecasts commonly differ from the actual return by more than a factor of 3, and the investigators suggest that better knowledge of sea conditions affecting survival and age at return is essential for improving these forecasts.

Within-season forecasts are sometimes the best that can be obtained but they usually require precise information on run timing. David Blackbourn reports that a considerable amount of the variation in the timing of Fraser River sockeye is explained by sea surface temperature anomalies in areas occupied by these stocks in the Gulf of Alaska. He also shows significant correlations between sea surface temperature and timing of several other Pacific Coast stocks.

Correct assignment of fish to respective stock groups is another high priority for the management of mixed-stock fisheries and scale pattern analysis (SPA) has been the principal tool for decades. SPA is laborious and often precludes the "real time" analysis essential for most contemporary fisheries management. Nevertheless, Marshall et al. have applied SPA succesfully to a wide range of mixed Alaskan sockeye stocks and Cook and Guthrie demonstrate considerable potential for fast automated equipment used by the International Pacific Salmon Fisheries Commission in 1985. Rapid dependable SPA automated equipment could be a major breakthrough for sockeye managers everywhere.

b) Management of some principal stocks

Strongly held fisheries management precepts often have a way of disintegrating in the light of extended or improved data sets. Minard and Meacham describe the historic Bristol Bay management system as seeking optimum escapements for each of the eight major river systems on the basis of spawner-recruit analyses. The predominant Kvichak run has a long history of cyclic trends in abundance with one or two major runs occurring in every four or five, and escapements have been regulated accordingly. However, the impressive simulation models of Eggers and Rogers suggest that the fishery acts to help maintain the cyclic trends and the authors recommend changing escapement goals and establishment of a second peak cycle run.

Cyclic dominance has also been a favourite theme on the Fraser River where sockeye return predominantly as 4-year old fish. Jim Woodey describes these runs as commonly having one dominant and two "off cycle" returns with high and low production, respectively. However, models described by Walters and Staley suggest that off cycle runs may be inherently as strong as dominant ones and point out that the observed cyclic trends in abundance, once established, could have been maintained by historical exploitation rates. They believe that generally higher escapements could lead to attractive improvements in yield from the Fraser River.

Sprout and Kadowaki state that Skeena River management must address the needs of more than 50 sockeye stocks, four other salmon species plus steelhead trout, all with overlapping timing, and exploitation by three principal gear types. Interception of Skeena sockeye by Alaskan fisheries, and undependable pre-season forecasts, make recognition and allocation of surpluses most difficult. Moreover, effective harvesting of the numerically dominant Babine stock puts smaller and less productive ones at risk.

Across the Pacific, Kamchatka sockeye are exploited by the Japanese high seas fisheries and by traps and drift nets as they enter the Kamchatka River. Viktor Bugaev describes stock dynamics and advocates higher escapements of some stocks accompanied by fertilization of the important Azabachye Lake. Exploitation rates should be varied according to thermal conditions prevailing during egg incubation because these conditions affect year class survival.

Michael Selifonov states that the Kamchatka and Ozernaya stocks together account for more than 90% of Asian sockeye production, and notes that harvests in excess of 75% of mature Ozernaya sockeye leads to declining production. He advocates reduction of the high seas fishery such that an escapement of 1.6–2.3 million spawners is achieved annually.

The once great Karluk Lake run collapsed from 4–5 to 0.5 million fish annually over 4–5 decades and prompted many extensive investigations and diverse proposals for a solution. Gard et al. present new evidence for the existence and genetic differentiation of sub-populations with characteristic run timings in Karluk Lake. Historical high production from mid-season spawners has been lost and these authors consider it unlikely that this group can be rebuilt from the remaining early and late spawning sub-populations. Meanwhile, Koenings and Burkett concur in the sub-population concept but believe that the major cause of sustained low production resides in the lake. They recommend balanced escapements to different run segments and lake enrichment to bolster growth and survival of early emerging fry.

Many sockeye stocks have disappeared and others have been gravely diminished by competition for water resources and by overfishing. Hyatt and Steer present a comprehensive history of sockeye production in Barkley Sound and conclude that a century of determined research and tenacious habitat protection and stock management have resulted in impressive gains in sockeye production from contributing stocks.

Colin Harris returns our thoughts to the high seas by tracing in exemplary detail the relationship of Japanese high seas fishing to changes in the USSR–Japan and the International North Pacific fisheries treaties. He concludes that changes in the amount and pattern of fishing in the late 1970's has greatly reduced the high seas catches of sockeye of both Asian and North American origin.

Finally, Peter Larkin recommends on the direction of future sockeye salmon research based on an entertaining review of several subject categories in the Journal of the Fisheries Research Board of Canada over the past four decades.

H. D. SMITH

Reference

BILTON, H. T. 1971. A hypothesis of alternation of age of return in successive generations of Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 513–516.

Introductory Presentation

Distribution and Abundance of Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

FORRESTER, C.R. 1987. Distribution and abundance of sockeye salmon (*Oncorhynchus nerka*). p. 2–10. *In* H.D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The general distribution of sockeye salmon (*Oncorhynchus nerka*) in the North Pacific region has been well defined over the years through studies conducted under the International North Pacific Fisheries Commission. The overlap in distribution of stocks from Asia and North America is also defined generally with overlap at least between 175°W and 170°E and between 46°N and about 58°N. Studies are continuing under INPFC to refine the limits of overlap. The abundance of sockeye was characterized historically by the existence of major stocks in Kamchatka, Western Alaska, Central Alaska, and the Fraser River system of southern British Columbia. Lesser stocks are found in adjoining areas, most importantly between Central Alaska and southern British Columbia. Greatest abundance originally was in Western Alaska and the Fraser River system. All stocks showed declines in abundance to low levels in the 1960's and 1970's. Catches in North American regions in very recent years have recovered to levels near or exceeding historical highs but catches from Kamchatka stocks have remained substantially below historic highs. Reasons for the recoveries or continued depression have not been considered in this paper.

Résumé

FORRESTER, C.R. 1987. Distribution and abundance of sockeye salmon (*Oncorhynchus nerka*). p. 2–10. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

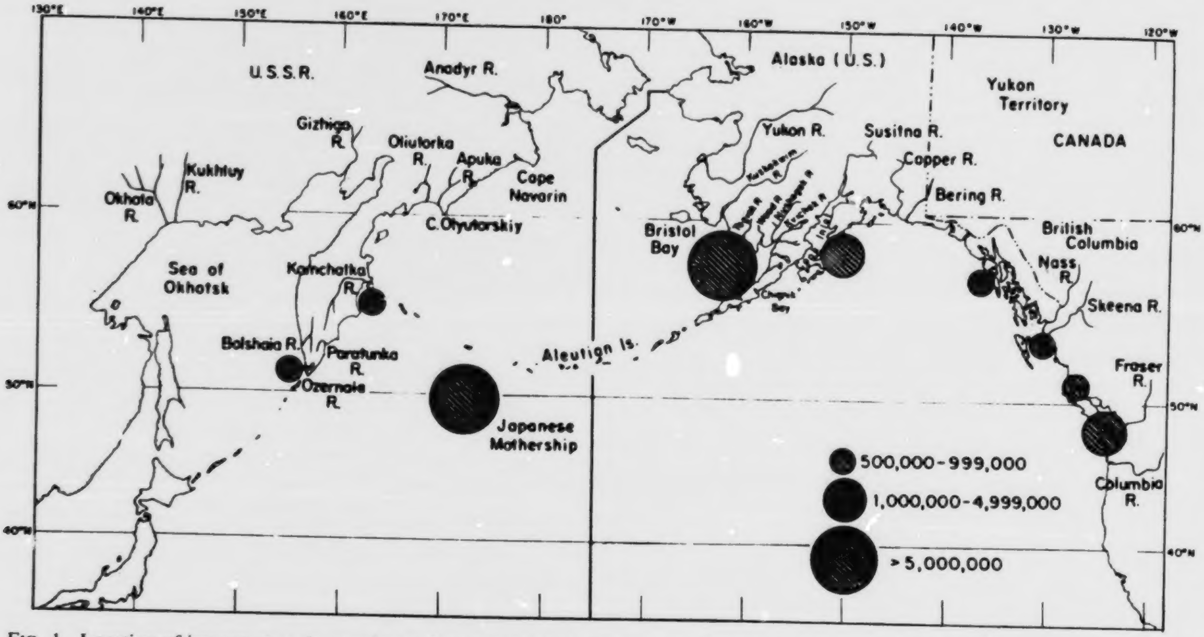
La distribution générale du saumon nerka (*Oncorhynchus nerka*) dans le Pacifique Nord a été bien définie au cours des années grâce à des études réalisées sous les auspices de la Commission internationale des pêcheries du Pacifique Nord. La zone de recouvrement des distributions des stocks de l'Asie et de l'Amérique du Nord est aussi assez bien définie. Cette zone s'étend au moins de 175°O à 170°E et de 46°N à environ 58°N. On continue à effectuer des études dans le cadre de la Commission afin de mieux définir les limites de cette zone de recouvrement. Par le passé, l'abondance du saumon nerka se caractérisait par l'existence d'importants stocks dans les régions du Kamchatka, de l'ouest de l'Alaska, du centre de l'Alaska et du bassin du fleuve Fraser dans le sud de la Colombie-Britannique. Des stocks moins importants se trouvent dans les zones adjacentes, notamment entre le centre de l'Alaska et le sud de la Colombie-Britannique. Les stocks les plus abondants se trouvaient autrefois dans l'ouest de l'Alaska et le bassin du fleuve Fraser. Tous les stocks ont décliné pour atteindre de bas niveaux au cours des années 60 et 70. Les prises effectuées dans les zones nord-américaines ont augmenté au cours des dernières années pour atteindre ou même dépasser les valeurs maximales antérieures, mais les prises des stocks du Kamchatka sont demeurées passblement inférieures aux prises historiques maximales. La communication ne traite pas des raisons du rétablissement ou du déclin continu de ces stocks.

The sockeye salmon, *Oncorhynchus nerka* (Walbaum), while not numerically dominant, is commercially the most valuable of the seven species of Pacific salmon, genus *Oncorhynchus*, native to the North Pacific region. This species is distributed generally between 44°N and 61°N from the southern Kurile Islands northward on the Asian coast, through the Bering Sea, and southward along the North American coast to the Columbia River (French et al. 1976) (Fig. 1).

Determination of relative abundance of sockeye in areas of the North Pacific requires some knowledge of magnitude of particular stocks. In simple terms, stock size is the sum of commerial catch from that stock and the remaining escapement to rivers of origin. Escapement data are not available for all stocks or for any stock for any lengthy time period. For that reason some measure of abundance has been presumed to be the magnitude of commercial catches that in early years, and with the exception of those on the high seas, were taken by fisheries operating fairly close to areas of origin of sockeye.

Distribution and abundance in Asia

On the Asian coast the bulk of the commercial catch of sockeye before 1945 came from stocks in Kamchatka, the principal rivers of origin being the Ozernaya and the Kamchatka. Early fishing was conducted mainly by Japan in U.S.S.R. coastal waters, with a peak in catch of about 15.4


130°E
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150°W
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120°W
60°N
50°N
40°N
U.S.S.R.
Anadyr R.
Alaska (U.S.)
Yukon Territory
CANADA
Gizhiga R.
Oliutorka R.
Apuka R.
Cape Navarin
C. Olyutorskiy
Kukhtuy R.
Okhota R.
Sea of Okhotsk
Kamchatka R.
Bolshaia R.
Paratunka R.
Ozernaia R.
Aleutian Is.
Japanese Mothership
Yukon R.
Susitna R.
Copper R.
Bering R.
Bristol Bay
Chignik Bay
British Columbia
Nass R.
Skeena R.
Fraser R.
Columbia R.
500,000-999,000
1,000,000-4,999,000
>5,000,000

FIG. 1. Location of important sockeye salmon river systems and average annual commercial catch of sockeye salmon (in numbers of fish) in important coastal and high seas fishing areas, 1961–71 (from French et al. 1976).

million fish in 1928: 12.0 million by Japan and 3.4 million by the U.S.S.R. (INPFC 1979; French et al. 1976).

In 1929, Japan established a mothership salmon fishery off Kamchatka and in 1933 driftnet and trap fisheries for salmon in the North Kurile region. Catches of Asian origin sockeye by the coastal fisheries of Japan and the U.S.S.R. and the newly established Japanese fisheries rose to 20 million fish in 1934: 15.8 million by Japan and 4.2 million by the U.S.S.R. (INPFC 1979; Fredin 1980).

Sockeye catches by Japan and the U.S.S.R. declined during the war years but increased rapidly with expansion of the new Japanese mothership fishery that had been organized in 1952. Over 15 million sockeye of Asian origin were caught in 1957, principally by the Japanese mothership fishery operating in a geographical area greatly expanded from that fished in 1952 (Manzer et al. 1965; Fredin 1980). Fukuhara (1975) noted that Japan's total mothership catch in 1957 (20.1 million fish) accounted for half of the world's sockeye landings for that year.

Catches of Asian sockeye declined to about 5 million sockeye in the 1970–76 period. The reduced catches were partially the result of imposition of quotas for salmon set by the Soviet–Japan Fisheries Commission first in 1957 that were gradually lowered in subsequent years (C.K. Harris, Fisheries Research Institute, University of Washington, Seattle, pers. comm.). The restrictions had the greatest impact, with respect to sockeye, on Japanese high seas catches but there was no corresponding increase in Soviet catches of sockeye. Soviet catches averaged 1.3 million sockeye during 1961–70 and only 0.5 million during 1971–77 (Fredin 1980).

Fredin (1980) estimated that during 1956–65 about 3 million sockeye of North American origin were also taken annually by the Japanese mothership fishery. However, the magnitude of the catches of sockeye of North American origin declined with adjustments to the fishery during 1974–77 (Rogers 1983) and even further in recent years following amendments in 1978 to the International Convention for the High Seas Fisheries of the North Pacific Ocean. Those amendments greatly reduced the geographical area of operation of the Japanese mothership fishery and limited its fishing effort. By 1982, Japan's catch of sockeye was only 2.5 million fish and Soviet catches were only 70% of that level (INPFC 1985; FAO 1984). Japan's catch of sockeye presumed to be of North American origin was reduced to 300,000 fish or less per year during 1982–85 (M. Dahlberg U.S. National Marine Fisheries Service, Auke Bay Alaska, pers. comm.).

Little information is available on total run sizes to Asian rivers, but it is generally accepted that the levels of commercial catches sometimes greatly exceeded those of escapement.

Distribution and Abundance in North America

North America commercial catches of sockeye have always been higher than Asian. Trends in overall abundance have been heavily influenced by the large runs to river systems in Bristol Bay, western Alaska. The most important of these systems are the Naknek, Kvichak, and Wood. During the period 1893–1971 annual commercial sockeye catches in Bristol Bay ranged from just under 1 million to almost 25 million fish and averaged 11.4 million (INPFC 1979). There were sharp peaks and decided lows in production despite the mid-1920's Federal legislative intent to allow in most streams 50% of the salmon to escape to spawn and thus theoretically maintain stocks (Crutchfield and Pontecorvo 1969). By 1947, the decline in some Alaskan salmon stocks to half that of levels only 10 years prior prompted Alaskan interests to establish and finance the Fisheries Research Institute in conjunction with the graduate school of the University of Washington to study biological problems of Alaskan salmon.

Catches of Bristol Bay sockeye dropped to an average of about 3.3 million fish during 1972–77 partly because of reduced ocean survival of fry during the cold winters of 1970–71 and 1971–72 (Rogers 1983) and the restrictions imposed on fishing effort designed to rebuild depressed stocks (Alaska Geographic 1983). During the mid to late 1970's, Japan also reduced the scope of its high seas mothership fishery and this resulted in reduced catches of Alaskan origin sockeye salmon (Fredin 1980; Rogers 1983). Subsequent increased escapements and increased juvenile survival have resulted in a rebound in stock sizes. Commerical catches of Bristol Bay sockeye averaged 22 million fish (range 15 to 26 million) during 1979 to 1982 and catches of 37 and 25 million fish were made in 1983 and 1984, respectively (Alaska Department of Fish and Game 1983, 1985). Preliminary estimates of escapement for the 1984 runs totalled 16 million sockeye. The Bristol Bay sockeye runs in 1985 were also at high levels with estimated catches of about 23.5 million fish and escapement of 13 million fish (Alaska Department of Fish and Game 1986). Thus, Bristol Bay stocks have returned to, and may now even exceed, the previous high historic levels of abundance implied from catch, although some river systems of the region have not responded as dramatically as others.

The Bristol Bay sockeye catches represented about 60% of the total Alaskan catch of sockeye during 1973–82 (Alaska Geographic 1983). Less important, but still significant runs were fished in the Cook Inlet, Chignik, Prince William Sound, and Kodiak areas of Central Alaska and in Southeastern Alaska.

Commercial catches of sockeye from Central Alaska ranged from 4 to 11 million fish annually during the period 1893 to 1952 but declined to approximately half those values in the succeeding 20 or so years (INPFC 1979). In the early years of exploitation, the Karluk system in the Kodiak district of Central Alaska was most important, producing an average annual catch of 1.9 million sockeye during the years 1887 to 1928 (Alaska Geographic 1983). Catches from this system declined sharply to levels around 0.5 million during the early 1950's and have remained at relatively low levels in recent years. On the other hand, Cook Inlet sockeye catches, mainly from the Kenai and Susitna river systems, have remained reasonably constant and during 1973–82 averaged 1.6 million fish. Chignik district sockeye catches in early years were one half or less of the level of those from the Kodiak district, but during 1973–82 averaged 1.2 million fish, almost twice the catch from Kodiak in the same period. In Prince William Sound, average sockeye catches during 1973–82 averaged 0.8 million fish. There has been no marked long-term trend in Prince William Sound catches, most of which originate from the Copper River (INPFC 1979; Alaska Geographic 1983). Sockeye catches from Central Alaska as a whole have increased markedly in recent years (Rogers 1983). Average annual sockeye catch during 1983–85 was 10.8 million fish (Alaska Department of Fish and Game 1983, 1985, 1986). Thus, Central Alaska sockeye stocks, as measured by commercial catches, have also rebounded to levels which equal or exceed the previous historic highs, but, as in the Bristol Bay region, the recovery has not been evident in all river systems.

In Southeastern Alaska, a number of small river and lake systems have sockeye runs that contribute to the commercial catch. In years prior to 1940 annual catches exceeding 2 million sockeye were not uncommon. Average annual catches dropped to 1.5 million fish during 1940 to 1945 and fluctuated at levels generally lower than one million through 1978. Sockeye catches since that time have shown an upward trend and in 1985 totalled approximately 1.8 million fish (INPFC 1979; Alaska Geographic 1983; Alaska Department of Fish and Game 1983, 1985, and 1986).

The statewide catch of Alaskan sockeye during 1973–82 averaged 19 million annually but increased to over 52 million in 1983, and 38 million in both 1984 and 1985. The 1985 catches were part of the largest estimated total harvest of salmon ever in Alaska's history (Alaska Department of Fish and Game 1986).

In the region south of Alaska the most important sockeye stocks are found in the Nass and Skeena systems of northern British Columbia, in the Rivers Inlet area of central British Columbia, and in the Fraser River system in southern British Columbia. The Nass and Skeena systems yielded an average of 0.7 million sockeye per year during the period 1951–62. Rivers Inlet area during the same period yielded an average of one million sockeye. The Fraser system, prior to the Hell's Gate slide in 1913, was often considered the greatest single area of sockeye production in the world and the dominant runs which occurred every four years were referred to as the "1901 cycle" (Aro and Shepard 1967). The Fraser River catches yielded a canned sockeye pack by Canada and the United States of almost 2.4 million 48-lb cases in 1913 (Kasahara 1953), which was roughly equivalent to 24 million fish[1]. Catches of sockeye from the Fraser declined sharply as a combined result of the slide and intensive exploitation (Thompson 1945; Kasahara 1963, Table 65) and did not recover appreciably until after 1946 when effective fishways were installed at Hell's Gate and rehabilitation of upstream sockeye stocks began to be vigorously pursued. Annual commercial production of sockeye in British Columbia during the period 1920 to 1976 was about 4.4 million fish compared to Alaska's 18.0 million during the same period (INPFC 1979). In the years 1977 to 1984, average British Columbia sockeye catch was 6.4 million fish (Anon. 1984). Henderson et al. (1984), in their reconstruction of British Columbia sockeye catch statistics for 1970 to 1984, note the continued influence of the 4-yr cycle in Fraser stock abundance on total British Columbia catches, although the dominant year in Fraser catches is now the one prior to the dominant year of pre-slide days. They also note a stable or increasing trend in the major producing stocks in British Columbia.

The 1985 catches of sockeye destined for the Fraser River, 11.7 million fish, were unusually high for this post-slide nonpeak year and escapement levels, which totalled 2.1 million fish, in some upstream Fraser areas (notably the Horsefly region) exceeded expectations (J. Woodey, Pacific Salmon

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[1] Foerster (1968) estimated that about 70-lb of raw sockeye yielded one 48-lb case. He also noted weights to 8-lb for Fraser River sockeye in early years. Average weights for B.C. sockeye in 1951–56 were about 6.45-lb (INPFC 1979). In the above estimate, average weight was assumed to be 7-lb, i.e., 10 fish per 48-lb case.

Commission, New Westminster, B.C., pers. comm.). Thus, the total Fraser sockeye run appears to be returning to historical high levels.

Catches of sockeye in United States waters south of British Columbia occur primarily adjacent to Washington State from stocks destined for the Fraser River system, though some smaller stocks also originate in the Puget Sound area and a few Washington coastal streams. Average catches were high during early years of the fishery (prior to 1918) but decreased as Fraser sockeye abundance declined. United States catches of sockeye from the Fraser system, under regulation by the International Pacific Salmon Fisheries Commission, have largely mirrored those of Canada, and have averaged 1.6 million fish during the past 20 years (1965 to 1984). No catches of sockeye of numerical importance are made in waters south of Washington State where stocks are small (Atkinson et al. 1967).

Comparison of abundance

It is difficult to determine accurately the relative abundance of sockeye from the greatly fluctuating commercial catches but it is generally accepted that the abundance of sockeye is much greater in North American stocks than in those of Asia. In the early historical data, catches were reported in numbers of fish, in tons landed, and in some regions in number of cases canned. Catches of Asian sockeye originating from the Kamchatka regions of greatest abundance were 7 million fish in 1920 (Foerster 1968) and increased to 20.1 million by 1934 as the Japanese mothership and driftnet fisheries developed (INPFC 1979). In Alaska, Bristol Bay sockeye catches were of the order of 24 to 25 million fish in a number of years between 1917 and 1938, and in Central Alaska sockeye catches were consistently between 5 and 10 million per year from 1893 to 1950 (INPFC 1979). The Fraser River system of British Columbia yielded catches bordering on 24 million fish in pre-slide (before 1913) years.

Thus, these four regions appear to be centers of historically greatest abundance. Catches from all regions showed a general decline from their historical highs. Low points in catches occurred in the early 1970's in Alaska and the early 1960s in British Columbia (Fredin 1980; Table 1). Sockeye in the Bristol Bay area, Central Alaska, and the Fraser system appear to be returning to, or exceeding, historical high levels of abundance, but this does not appear to be the case for Asian (Kamchatka) stocks.

Offshore distribution

JUVENILES

Studies have shown that juvenile age .0 sockeye generally begin to enter the open ocean in June (Hartt and Dell 1986). During their first ocean summer, off North America

TABLE 1. Mean annual catches of sockeye (millions of fish) from certain regions of the North Pacific, 1901 to 1985.

Period or year	Country or region						
			Alaska				
	Japan	U.S.S.R.	Total	Western	Central	B.C.[a]	Wash.-Ore[a]
1901-1905	—	—	21.17	13.22	5.65	(5.95)	(5.55)
1906-1910	—	—	21.04	12.97	5.44	(5.07)	(3.36)
1911-1915	1.68	—	26.08	17.73	5.46	(5.63)	(5.02)
1916-1920	3.96	—	27.85	17.40	7.68	(3.10)	(1.64)[b]
1921-1925	7.43	—	24.25	16.00	6.21	4.11	0.91
1926-1930	8.43	3.49[c]	21.13	13.90	5.37	3.94	1.36
1931-1935	9.36	2.75	23.58	15.74	6.31	3.89	1.32
1936-1940	13.60	?	27.33	17.70	7.41	4.56	0.94
1941-1945	7.48	2.77	17.75	10.30	5.89	4.22	1.34
1946-1950	—	3.33	17.26	11.33	5.29	4.27	1.55
1951-1955	2.25	2.02	11.35	6.63	3.69	4.95	2.11
1956-1960	12.57	1.27	11.34	8.00	2.44	4.89	2.26
1961-1965	7.57	1.57	14.27	10.14	3.29	3.36	1.04
1966-1970	7.36	1.03	14.17	9.01	4.29	5.07	1.52
1971-1975	4.99	0.54	7.52	4.06	2.76	4.94	2.25
1976-1980	3.58	(0.90)[d]	20.88	14.23	5.72	5.44	1.39
1981	3.07	(1.31)[d]	36.36	27.57	7.70	8.44	1.33
1982	2.46	(1.01)[d]	29.12	16.80	10.83	10.08	2.88
1983	(2.48)[e]	?	52.36	39.38	11.43	5.52	0.40[e]
1984	(1.90)[e]	?	38.16	26.52	10.47	5.08	1.71[g]
1985	(1.29)[e]	?	38.38	26.11	10.42	12.25[f]	2.82[g]

[a] British Columbia and Washington-Oregon catches for 1901-20 estimated from canned sockeye pack data given in Kasahara (1963). See footnote 1 in text.

[b] Estimate from canned pack data of Kasahara (1963, table 68) equals 1.42 million, compared to 1.64 million average from data in table 80 of INPFC 1979.

[c] 1927-30 mean.

[d] Estimated from FAO statistics in tonnes and average weight of 2 933 g/fish shown in table 3-1 of INPFC 1979.

[e] Preliminary estimate from INPFC Yearbooks in preparation.

[f] Personal communication, M. Kostner, Canada Department of Fisheries and Oceans, Vancouver, B.C.

[g] Personal communication, D. Ward, Washington State Department of Fisheries.

they become distributed in a continuous belt in coastal areas adjacent to all areas of production from Cape Flattery to the eastern Aleutians and in the Bering Sea. They may migrate extensively within this belt (French et al. 1976). By September abundance decreases in the southern and eastern Gulf of Alaska, but increases south of the Alaska Peninsula and eastern Aleutians and in the Bering Sea. Off Kamchatka there was some suggestion that dispersion of age .0 sockeye offshore from this region and from the Sea of Okhotsk is slightly later than off North America (French et al. 1976).

Limited sampling during winter months (after January 1), has shown that age .1 sockeye by then disperse widely in

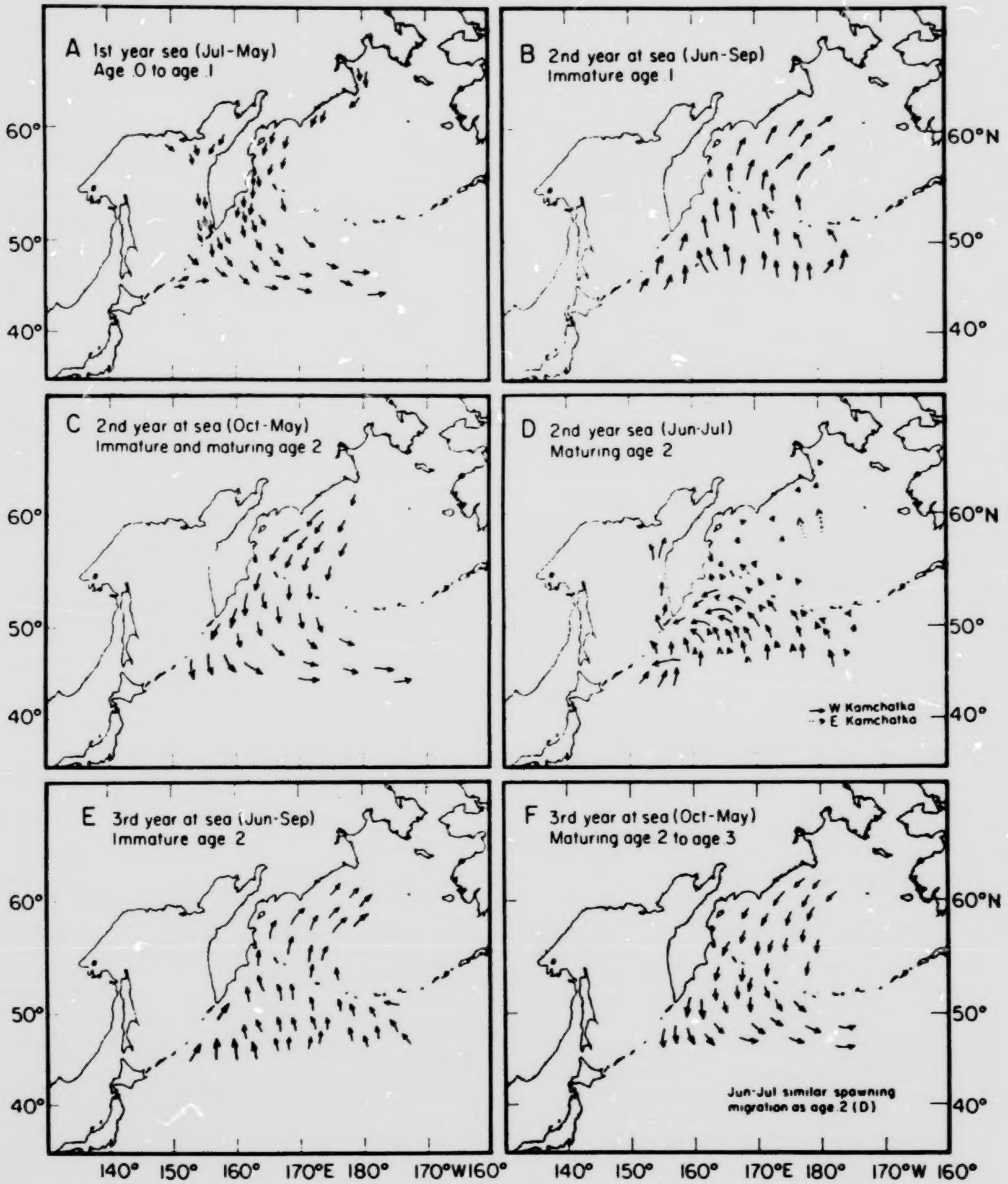
A 1st year sea (Jul-May)
Age .0 to age .1
B 2nd year at sea (Jun-Sep)
Immature age .1
C 2nd year at sea (Oct-May)
Immature and maturing age 2
D 2nd year sea (Jun-Jul)
Maturing age 2
→ W Kamchatka
⇢ E Kamchatka
E 3rd year at sea (Jun-Sep)
Immature age 2
F 3rd year at sea (Oct-May)
Maturing age 2 to age 3
Jun-Jul similar spawning migration as age 2 (D)
60°
50°
40°
60°N
50°
40°
140°
150°
160°
170°E
180°
170°W
160°

FIG. 2. Model of migration of Asian sockeye salmon (from French et al. 1976).

the North Pacific almost to the limits of their distribution, with the main body of fish occurring between 46° and 50°N and 175°E and 155°W. By late spring, age .1 sockeye are dispersed widely in the Gulf of Alaska north of 46°N and along the Aleutians as far west as sampling was conducted, but they are not abundant in the western North Pacific. With the approach of summer the age .1 sockeye move north and by July are found mainly north of 50°N with patches of high abundance apparent in the western Bering Sea and off Kamchatka near the end of the Aleutian Chain. By this time the

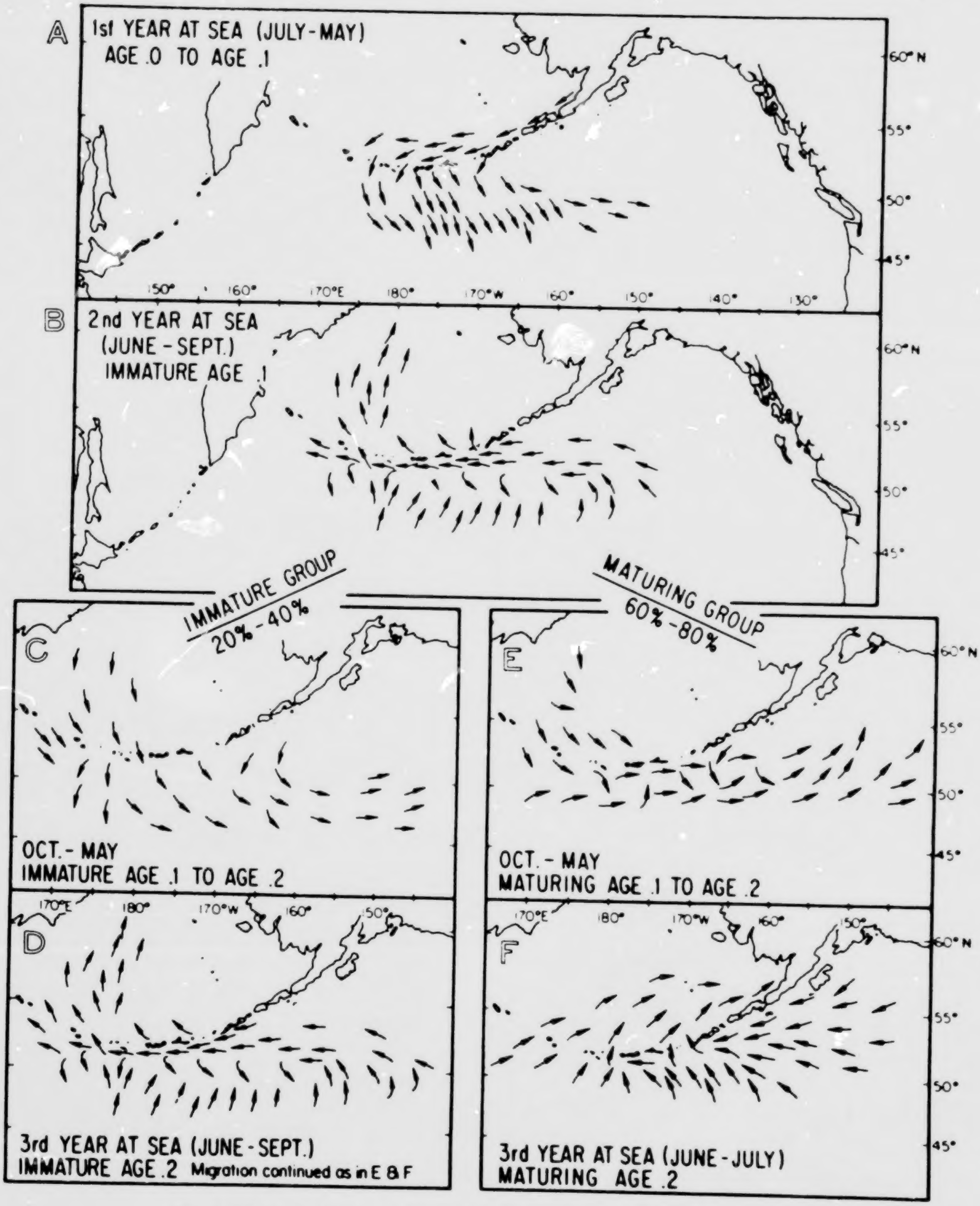
A
1st YEAR AT SEA (JULY-MAY)
AGE .0 TO AGE .1
60°N
55°
50°
45°
150°
160°
170°E
180°
170°W
160°
150°
140°
130°
B
2nd YEAR AT SEA
(JUNE-SEPT.)
IMMATURE AGE .1
60°N
55°
50°
45°
IMMATURE GROUP
20%-40%
MATURING GROUP
60%-80%
C
OCT.-MAY
IMMATURE AGE .1 TO AGE .2
E
OCT.-MAY
MATURING AGE .1 TO AGE .2
60°N
55°
50°
45°
D
170°E
180°
170°W
160°
150°
3rd YEAR AT SEA (JUNE-SEPT.)
IMMATURE AGE .2 Migration continued as in E & F
F
170°E
180°
170°W
160°
150°
60°N
55°
50°
45°
3rd YEAR AT SEA (JUNE-JULY)
MATURING AGE .2

FIG. 3. Model of migration of western Alaska sockeye (from French et al. 1976).

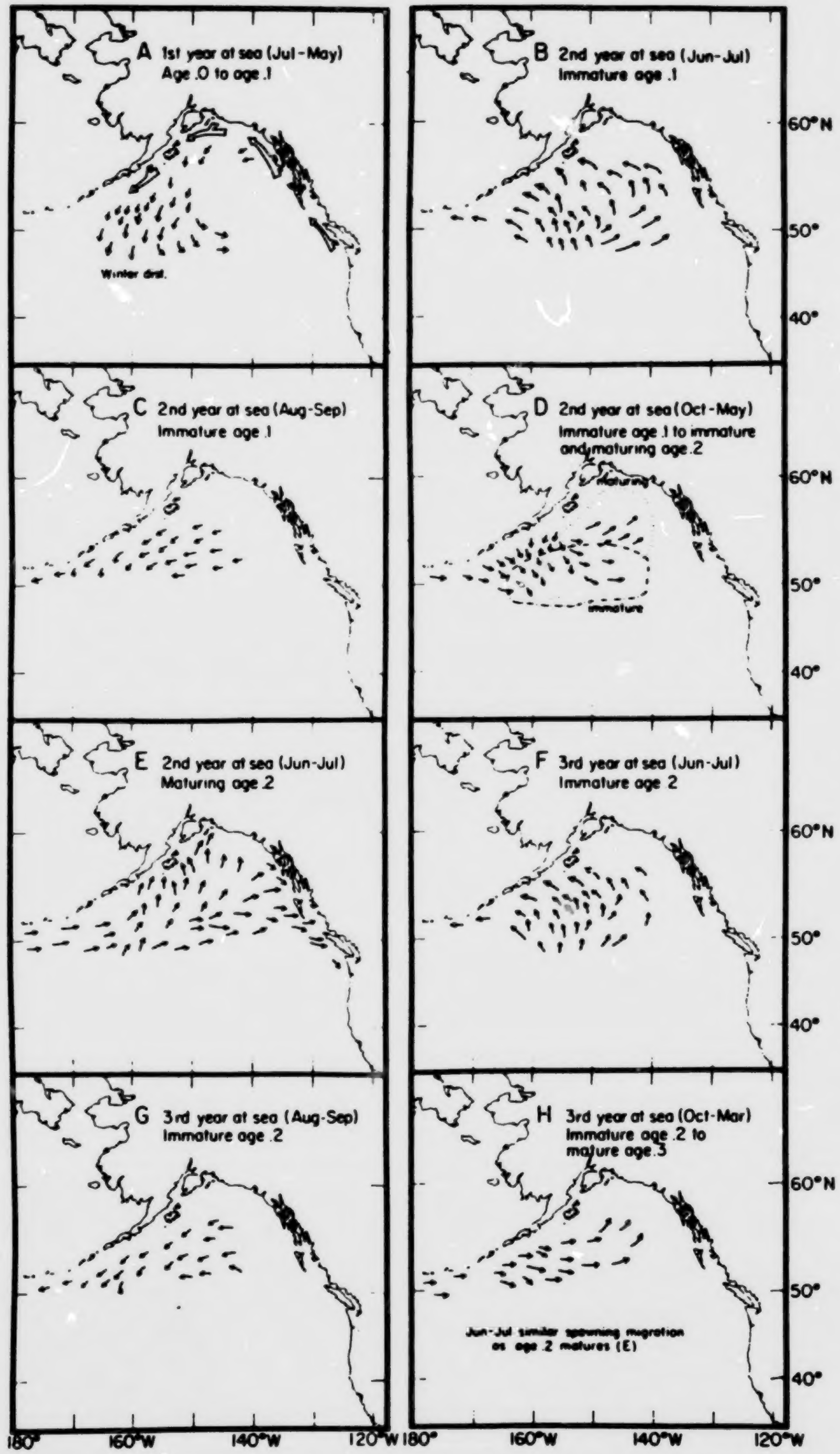
A 1st year at sea (Jul-May)
Age .0 to age .1
Winter dist.
B 2nd year at sea (Jun-Jul)
Immature age .1
C 2nd year at sea (Aug-Sep)
Immature age .1
D 2nd year at sea (Oct-May)
Immature age .1 to immature and maturing age .2
Maturing
Immature
E 2nd year at sea (Jun-Jul)
Maturing age .2
F 3rd year at sea (Jun-Jul)
Immature age .2
G 3rd year at sea (Aug-Sep)
Immature age .2
H 3rd year at sea (Oct-Mar)
Immature age .2 to mature age .3
Jun-Jul similar spawning migration as age .2 matures (E)
60°N
50°
40°
180°
160°W
140°W
120°W

FIG. 4. Model of migration of northeastern Pacific sockeye salmon (from French et al. 1976).

following year-class of sockeye makes its appearance in the ocean as age .0 fish but there is little overlap with distribution of age .1 fish. In the fall, the limited sampling suggested a southward and eastward movement of age .1 fish with abundance most pronounced south of the western Aleutians and in the Gulf of Alaska.

AGE. 2 IMMATURE SOCKEYE

In winter, January to March, the age .1 fish of the previous year can be described as age .2 "immatures" with distribution similar to that for age .1 of the succeeding year-class. The majority were distributed south of 52°N, none were found in the Bering Sea, and none were caught in the limited sampling west of 175°E. By spring the sockeye were again moving northward and westward, and age .2 fish are distributed farther north than age .1 sockeye. The pattern of retreat southward and eastward with the approach of fall and winter was repeated by the age .2 immature fish.

MATURING FISH

In winter, distribution of maturing age .2 fish overlapped with immatures of both age .1 and .2, but greatest concentrations of maturing fish are 2° to 3° farther north. By spring, the center of abundance of age .2 maturing sockeye is north of 50°N and by June homeward migration appears to be well advanced. By summer, high seas catches are low except near shore.

Also in winter, age .3 sockeye are virtually all maturing and widely distributed in the northern North Pacific and Bering Sea. They are northward of the maturing age .2 fish and the immature age groups. By late spring, the age .3 fish had mainly migrated homeward from offshore waters.

General Aspects of Distribution

Temperature is the greatest determinant of the general limits for southward distribution of sockeye in the North Pacific. Southern limits generally occur where mean sea surface temperatures are about 12° to 13°C in summer and 7° to 8°C in winter and abundance is generally not significant at sea surface temperature higher than 10° or 11°C (French et al. 1976; Burgner and Meyer 1983). Their northward distribution (in general to a maximum of about 61°N) is probably limited by low temperatures that may influence growth and thus survival (Straty 1981).

While at sea, the sockeye have a broad oceanic distribution extending over most of the North Pacific Ocean and Bering Sea from about 44°N to near 61°N and have migrated for many thousands of kilometers. Their vertical distribution during this period has been primarily within 15 meters of the surface (French et al. 1976).

Overlap in Distribution of Asian and North American Sockeye

The high seas overlap in distribution of Asian and North American sockeye has been the subject of much research within the International North Pacific Fisheries Commission. These ongoing studies have utilized results of tagging studies, stages of gonad development, prevalence of parasites, etc. (Takagi 1961; Margolis et al. 1966) and shown an area of intermingling at least between 175°W and 170°E and between 46°N and about 58°N. The models of migration of sockeye of Asian, Western Alaska, and northeast Pacific origin, reproduced here as Fig. 2, 3, and 4, were prepared by French et al. (1976) from results of these studies. Studies

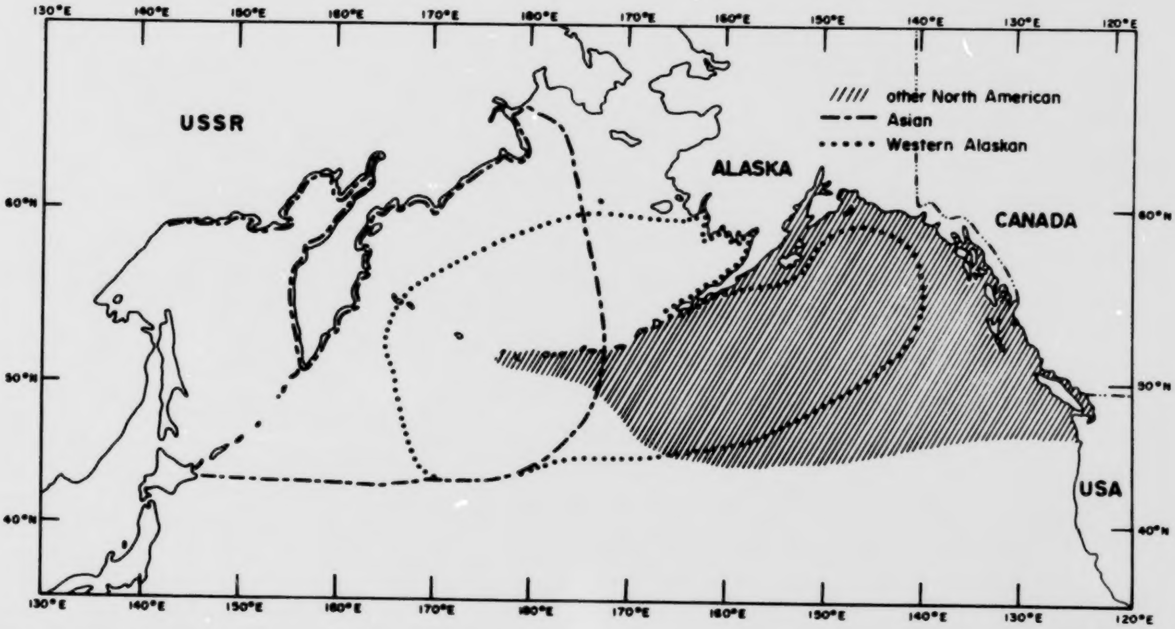

FIG. 5. Generalized ocean distribution of sockeye salmon from Asia, western Alaska and other North American areas (from French et al. 1976, modified).

of overlap in distribution have continued (see INPFC Annual Reports 1979–84, inclusive, and their references to research on salmonids), and a joint comprehensive three-nation report is in preparation summarizing new findings on distribution (INPFC 1982 Annual Report, p. 7). The general distribution of sockeye salmon in the North Pacific has been quite well defined over the years (Fig. 5). However, distribution of fish from the various regions is less well known. Studies in that direction are continuing as are those on departures from normal distribution paths when the sockeye are homeward bound.

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Section I
Biology of Sockeye Salmon
a) Life History Strategies

Alternative Juvenile Life Histories of Sockeye Salmon (*Oncorhynchus nerka*) and Their Contribution to Production in the Stikine River, Northern British Columbia

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Abstract

Wood, C. C., B. E. Riddell, and D. T. Rutherford. 1987. Alternative juvenile life histories of sockeye salmon (*Oncorhynchus nerka*) and their contribution to production in the Stikine River, northern British Columbia, p. 12–24. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Juvenile sockeye salmon (*Oncorhynchus nerka*) typically rear in lakes for 1 or more years before migrating to sea ("lake-type" sockeye), but particularly in northern populations, some individuals go to sea shortly after emergence ("sea-type" sockeye), or inhabit river channels for at least 1 year ("river-type" sockeye). The prevalence of these alternative life history phenotypes was investigated during 1983–85 for six populations spawning in three distinct habitats within the Stikine River watershed. Sea-type and river-type sockeye were distinguished by their scale and otolith structure. Sea-type sockeye were not found in spawning areas with access to lakes but comprised an average of 15.4% (range 2–55%) of spawners in tributaries not associated with lakes. Size-frequency data suggest that sea-type sockeye in the Iskut River migrated to sea at a mean weight of approximately 1 g whereas river-type sockeye migrated primarily as yearlings with a mean weight of 3 g. Lake-type sockeye emigrating from Tahltan Lake as 1+ smolt (97% of emigrants) averaged 3.6 g in 1985. The stock composition of adults migrating upstream through the lower Stikine River was estimated using electrophoretic, parasitic, age composition, and scale pattern characteristics. Sea-type and river-type sockeye, respectively, contributed 5% and 39–48% in 1984 and 1985, to the total return of adult sockeye to the Stikine. This study demonstrates the advantages of using multiple characteristics for stock identification and the potential significance of river-rearing habitat for northern sockeye populations.

Résumé

Wood, C. C., B. E. Riddell, and D. T. Rutherford. 1987. Alternative juvenile life histories of sockeye salmon (*Oncorhynchus nerka*) and their contribution to production in the Stikine River, northern British Columbia, p. 12–24. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Avant de migrer vers la mer, le saumon nerka juvénile (*Oncorhynchus nerka*) fréquente en général des milieux lacustres pendant une année ou plus (saumon nerka lacustre) mais on remarque que chez des populations septentrionales, certains individus se dirigent vers la mer peu de temps après leur émergence (saumon nerka marin) ou vivent en eau douce au moins 1 an (saumon nerka fluviatile). De 1983 à 1985, les auteurs ont étudié la fréquence de ces autres phénotypes en matière de cycle vital chez six populations frayant dans trois habitats distincts du bassin versant de la rivière Stikine. Les écailles et les otolithes ont servi à la différenciation des saumons nerkas marins et fluviatiles. Le saumon nerka marin n'était pas présent dans les frayères des tributaires de lacs mais représentait, en moyenne, 15,4 % (écart : 2–55 %) des reproducteurs présents dans les tributaires sans accès à un lac. Les données sur la fréquence des tailles portent à croire que le saumon nerka marin de la rivière Iskut migre vers la mer à un poids moyen d'environ 1 g tandis que le saumon nerka fluviatile migre à l'état de saumon d'un an quand son poids moyen atteint 3 g. Pour sa part, le saumon nerka lacustre a quitté le lac Tahltan à l'état de smolt de 1+ an (97 % des migrateurs) à un poids moyen de 3,6 g en 1985. Les données recueillies au cours d'études par électrophorèse, des parasites, de la composition par âge et des écailles ont servi à l'estimation de la composition du stock d'adultes amontants dans la partie inférieure de la rivière Stikine. En 1984 et 1985, les saumons nerkas marins et fluviatiles composaient respectivement 5 % et de 39 à 48 % de la remonte totale de saumons nerkas dans la rivière Stikine. La présente étude révèle les avantages de l'utilisation de caractéristiques multiples pour l'identification de stock et l'importance potentielle des aires de croissance en milieu fluvial pour les populations septentrionales de saumon nerka.

Introduction

Sockeye salmon (*Oncorhynchus nerka*) are unique among Pacific salmon in that juveniles typically spend at least one summer rearing in lakes. Sockeye populations are, however, highly variable with respect to age-at-maturity and the length of time juveniles inhabit fresh water (e.g., Foerster 1968). There is also growing evidence that juvenile sockeye utilize riverine and estuarine habitat for rearing where lake habitat is unavailable; indeed, lake-rearing behaviour may not be typical for many sockeye populations in northern areas.

Gilbert (1918) inferred, from scale patterns, that sockeye salmon fry emerging in the Harrison Rapids below Harrison Lake, British Columbia migrated to sea as underyearlings. He did not find these "sea-type" sockeye elsewhere in the Fraser River watershed. Apparently, the underyearling (age 0+) sockeye inhabit slackwater areas of the Fraser River estuary for many months (Birtwell et al. 1987). Ward (1921) observed sockeye salmon spawning in Clear Creek, a tributary of the Copper River, Alaska, where emerging fry would not have access to a limnetic rearing habitat; the occurrence of sockeye with sea-type scale patterns in the Copper River and adjacent streams has since been confirmed (Sharr et al. 1984). Sea-type sockeye have also been observed in other Alaskan rivers, especially in the Yakutat area and the Nushagak River (S.L. Marshall, Alaska Department of Fish and Game, Anchorage, Alaska, pers. comm.), and to a lesser extent in southeastern Alaska (McGregor 1983). In Kamchatka, sea-type sockeye occur in the Bolshaya River (Semko 1954), the Paratunka River (Krogius 1958), and the Kamchatka River (Krokhin and Krogius 1937; Bugaev 1984, 1987). Juvenile sockeye salmon are also known to rear for one or more years in lagoons or pools of the Bolshaya River (Semko 1954), the Kamchatka River (Krogius 1958), and the Stikine River in northern British Columbia (McCart and Walder 1982). Following Semko (1954) we refer to these as "river-type" sockeye salmon.

The purpose of this paper is to compare aspects of life history, growth, and overall production of sea-, river- and lake-type sockeye salmon in the Stikine River watershed. We compared sockeye populations found in three different habitats: a clear, interior lake typical of the Skeena or Fraser River watersheds (Tahltan Lake); two small, glacial lakes (Chutine Lake and Christina Lake); and three tributaries within which fry do not have access to lake rearing-habitat (the Iskut, Scud, and Chutine rivers). Until recently, the Tahltan Lake population was thought to comprise 90% of the total sockeye salmon run to the Stikine River (Bergmann 1978). We used differences in allozyme allele frequency, parasite prevalence, scale characteristics, and age composition to identify stocks individually, and conclude that river-type sockeye comprise over one third of the total run of adult sockeye within the Stikine River.

Study Area

The Stikine River watershed occupies 51 200 km^2 of which 98% lies in northwestern British Columbia and 2% in southeastern Alaska. The watershed is drained by two principal rivers — the Stikine and the Iskut rivers; both originate on a semi-arid plateau above 3 000 m elevation, about 450 and 250 km from the ocean, respectively, and flow southwest through rainforests of the heavily glaciated Coast Range Mountains (Fig. 1). Most of the clearwater tributaries and lakes associated with the plateau are inaccessible to salmon owing to velocity barriers, landslides, and natural falls. Most of the streams and lakes associated with the coastal mountains are glacial in origin and, consequently, very turbid. About 13 000 km^2 of the watershed is thought to be accessible to salmon, but over half of this is turbid due to glaciation. The remote location and turbidity of the mainstem Stikine and Iskut rivers and their glacier-fed tributaries precludes direct estimation of salmon populations in a large portion of the watershed. Few large lakes are accessible to anadromous salmon and only Tahltan Lake, which apparently supports the largest sockeye salmon population, provides a clearwater environment for juveniles. Sockeye escapements at Tahltan Lake have averaged 21 000 (maximum 67 000 in 1985) since 1959 when a weir was installed; no other sockeye runs within the watershed have been enumerated directly.

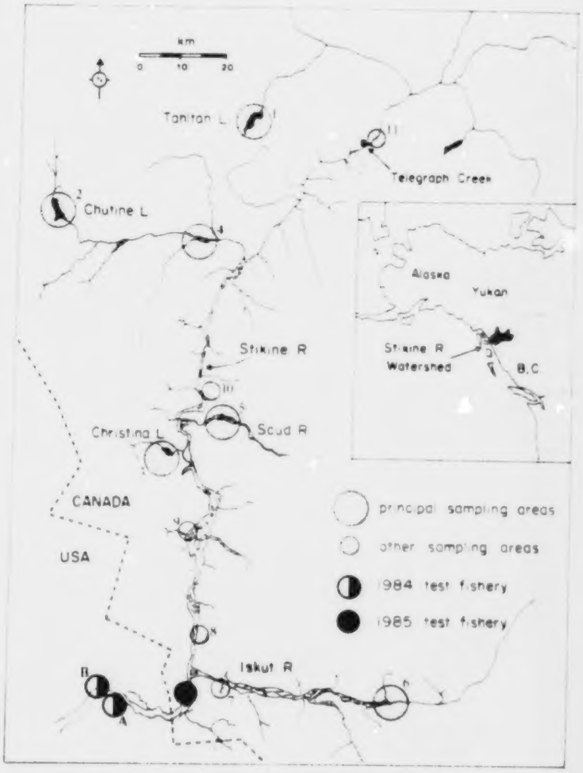

FIG. 1. Location of sampling sites for adult sockeye salmon in the Stikine River watershed. Site 4 is the Chutine River site.

Methods

SAMPLE COLLECTION

Adult sockeye salmon were collected from five principal spawning sites in the Stikine River and one in the upper Iskut River from August to September, 1982–85 (Fig. 1): Tahltan Lake (TAHL), Chutine Lake (CHUL), Christina Lake (CHRL), Chutine River (CHUR), Scud River (SCUR), and the Verrett River (VERR). Additional samples of spawning fish were obtained from the mainstem of the Stikine River below Christina Creek (site 9 in Fig. 1) in 1983, above its confluence with the Scud River (site 10), and just above its confluence with the Iskut River (site 8) in 1985. Length and sex data, scales, otoliths, brains, and tissues for electrophoretic analysis were obtained from 50 to 200 fish in each of the principal areas; only brains and otoliths were collected from the additional sites in 1985. Where possible, egg diameter and fecundity data were collected from specimens collected at TAHL, SCUR, and VERR in 1985. All fish were alive and judged to be spawning or to have completed spawning when captured. Sampling procedures and results are described in detail by Wood et al. (1987b).

Both fyke nets (2 × 2 × 7.5 m with graded meshes from 5.0 to 1.3 cm) and beach seines (30 × 3 m with 1.3-cm mesh) were used to collect juvenile sockeye salmon. Fyke nets were deployed as described by Hyatt et al. (1984) but proved ineffective due to high water levels and the quantity of debris in the river. A fyke net was operated on Christina Creek near the outlet of CHRL 24 h each day from May 27 to June 17, 1985 and in the lower Iskut River just upstream from the Stikine River on May 24, 1985; the latter net was destroyed by debris after 1 day. Juveniles were collected by beach seine from 10 different locations within 10 km of the Stikine–Iskut confluence and from CHRL during 1985. Growth of river-rearing juveniles was monitored in one slough in the lower Iskut River by repeated sampling from May 19 to Oct. 27, 1985; five other areas were sampled at roughly 2-wk intervals from late August to late October, 1985 (Fig. 2). Fork length of juveniles was measured before preservation; specimens from the fyke net at CHRL were frozen for later electrophoretic and parasite analysis. Scales were taken from all specimens collected in May and June, 1985, and from stratified random samples (five per 5-mm length interval) in subsequent collections. Smolts from TAHL were enumerated at the outlet weir and sampled daily for length, weight, and scales in 1984 and 1985.

Adult sockeye were collected from test fisheries in the lower Stikine River about 16 km below the Alaska–B.C. boundary in 1984 and about 3 km above the boundary in 1985 (see Fig. 1). In 1984, the Alaska Department of Fish and Game operated a sonar counter on one side of the river together with 12- and 13-cm mesh gillnets at both of two sites located on opposite sides of the river; site A on the south bank is believed to provide a more representative sample of the overall salmon run (B. Lynch, Alaska Department of Fish and Game, Petersberg, Alaska, pers. com.). Length, sex and egg-diameter data, scales, otoliths, and brains were collected from up to 200 fish per week between June 15 and August 15, 1984. A representative sample of the entire run was obtained by subsampling each week's (sampled) catch in proportion to the estimated magnitude of the run based on the sockeye-apportioned sonar counts; the representative samples include 248 sockeye from site A and 91 sockeye from site B.

In 1985, sockeye were collected using 12- and 13.3-cm mesh gillnets fished on different days at a single location for a 24-h period each week. Tissues for electrophoretic analysis (heart, liver, eyeball, and skeletal muscle) were collected in addition to data collected in 1984. All fish from the 12-cm mesh net were sampled to obtain a representative sample of the run based on a constant fishing effort. Due to excessive catches during the first 3 wk, the length of the net was reduced from 68 to 33 m for the remaining 9 wk. A random subsample of 50% was taken to represent the first 3 wk, resulting in a total sample of 661 fish. Up to 100 fish were sampled each week from the 13.3-cm mesh net; a representative sample of the entire run was obtained by subsampling each week's catch in proportion to the catch-per-unit-effort in the in-river commercial fishery where a similar mesh size was used. Two additional samples of 77 and 100 sockeye were collected wih 13.3-cm mesh gillnets in the lower Iskut River (site 7 in Fig. 1) on August 4 and August 10–14, 1985. These fish had not spawned and were assumed to be migrating to spawning grounds in the upper Iskut River. All fish were sampled for length, sex, scales, otoliths, brains, electrophoretic tissues, and where possible, egg diameter and fecundity. The same data were also collected from 302 specimens from the Telegraph Creek subsistence fishery (site 11) July 4–Aug. 14.

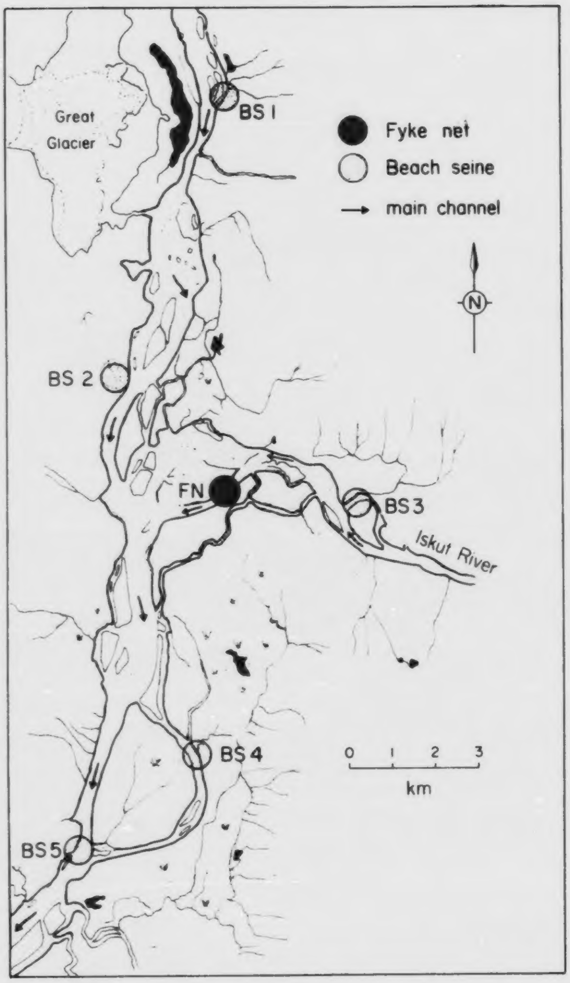

FIG. 2. Location of sites in the lower Stikine and Iskut rivers that were sampled regularly for juvenile sockeye salmon.

Procedures for age determination, interpretation of scale patterns, examination for the presence of the brain parasite *Myxobolus neurobius*, and electrophoretic analysis are reported in Wood et al. (1987b). Spawning ground samples were assayed electrophoretically at 24 loci but only 8 loci were polymorphic; these included phosphoglucomutase-1, -2 (PGM), lactate dehydrogenase-4 (LDH), isocitrate dehydrogenase-4 (IDH), aspartate aminotransferase-1, -3 (AAT), glucose phosphate isomerase-1 (PGI), and alpha-glycerol-3-phosphate dehydrogenase-1 (AGP). Test fishery samples in 1985 were assayed at only the 4 most variable loci (PGM-1, PGM-2, LDH-4, and IDH-4).

STOCK COMPOSITON ESTIMATES

Stock composition of the test-fishery samples was estimated using the maximum likelihood mixture model (e.g., Fournier et al. 1984). Learning samples were compiled for the 6 principal spawning sites (in Fig. 1) using various combinations of traits measured in the test fishery samples. For the 1984 fishery samples, each learning sample was characterized by age composition, prevalence of the brain parasite, and the number of circuli in scale zones 1–3 of age 1.3 fish (denoted NC(1), NC(2), and NC(3) after Marshall et al. 1984). Scale zone 1 included circuli formed during the first year in freshwater; zone 2 included only circuli formed during the second year prior to entering the sea ("plus growth"); and zone 3 included only circuli formed during the second year while at sea. These scale characteristics were poorly correlated with each other ($r < 0.29$ in test samples from the 1984 test fishery) and were assumed independent. The 1984 learning samples included parasite data from 1982 to 1984 since parasite prevalence was similar from year to year within sites (see Results). Only 1984 scale and age composition data were included because little information was available for other years and both characteristics often differ between brood years in other areas. Learning samples for analysing 1985 fishery data included parasite prevalence, freshwater-age composition and genotypic frequencies at four loci (PGM-1, PGM-2, LDH-4 and IDH-4). Pooled data from 1982 to 1985 were used since annual variation in the frequency distributions for each trait was much less than variation between stock spawning sites. There was a weak correlation between parasite prevalence and freshwater age (see Results) but these traits were also assumed independent.

To assess the accuracy of the mixture model, resampling procedures were used to generate, and then resolve, test mixtures of known composition. Sampling error was introduced, independently, to both the test mixtures and the learning samples used to resolve them, by random resampling with replacement from the observed learning samples (i.e., "bootstrapping", Efron 1982). The test mixtures consisted of 498–500 fish drawn from the six learning samples ("stocks") either in equal proportion such that each stock contributed 16.7% (83 fish), or with 50% (250 fish) drawn from TAHL and 10% (50 fish) drawn from the remaining stocks. To determine accuracy and precision, mean estimates (with standard deviations) were calculated from 100 estimates at each test mixture composition using various combinations of the available traits. Similarly, the mean and standard deviation of at least 100 bootstrapped estimates were obtained for each test fishery sample by resolving resampled mixtures with resampled learning samples; both the resampled mixture and learning sample sizes were identical to the observed samples.

To increase accuracy, the difficulty of the mixture problem was reduced by summing the estimated mixing proportions for each of the six principal stocks, sequentially, beginning with the most similar stocks, following the procedure suggested by Wood et al. (1987a). This involved computing distances in trait-space between all possible pair-wise combinations of stocks to construct a similarity dendrogram using the single linkage procedure (Pielou 1977). Both genetic and non-genetic traits were used to measure distance with a statistic resembling Nei's genetic distance (Nei 1972), which was evaluated by Wood et al. (1987a):

distance between stock i and stock j =

$$(1) \qquad \phi_{ij} = \left[\sum_{k} D_{ijk}^2\right]^{1/2}$$

where

$$(2) \qquad D_{ijk} = -\log_e \left[\frac{\sum_{\ell} P_{ik\ell}\; P_{jk\ell}}{\left(\sum_{\ell} P_{ik\ell}^2 \sum_{\ell} P_{jk\ell}^2\right)^{1/2}} \right]$$

and k indexes the trait and ℓ indexes the state within traits; $P_{ik\ell}$ is the relative frequency of state ℓ of trait k in the sample from stock i. The similarity dendrogram was robust to the choice of distance statistic and subset of traits used; a similar grouping sequence was obtained using only electrophoretic data and the unbiased genetic identity statistic (Nei 1978). We concluded that the most useful tradeoff between accuracy and stock resolution was achieved by summing estimates for the CHUR–SCUR–VERR group and for the CHUL–CHRL group thereby providing estimates of the overall contributions from Tahltan Lake, the two glacial lakes, and the tributaries without access to lake habitat.

Results

OCCURRENCE OF DIFFERENT JUVENILE LIFE HISTORIES

Freshwater age composition of spawning sockeye was highly variable among spawning sites and was generally consistent during both 1984 and 1985 (Table 1). No age 0. fish (i.e., lacking a freshwater check in scales and otoliths) were found in any of the spawning samples from TAHL, CHUL, and CHRL. Spawners from TAHL were predominantly age 1. (92 and 97% in 1984 and 1985, respectively). Age 2. spawners were most abundant in the glacial lake populations, CHUL and CHRL (43 and 57%, respectively, in 1984).

In contrast, age 0. spawners were found in all samples from river sites (sites 4–10). We assumed that these fish spent less than a full year in fresh water and conclude that they are sea-type sockeye. The majority of spawners in river sites were age 1.3 (range 64–94%) in both 1984 and 1985. We assumed that these fish spent at least 1 year in the main river channel or in slackwater sidechannels (sloughs) and conclude that they are river-type sockeye. The proportion of sea-type sockeye at river sites was higher in 1985 (20%) than in 1984 (6%). However, this may only reflect inadequate sampling since the overall contribution to the representative test fishery samples was 4.6 and 4.7% in 1984 and 1985, respectively.

TABLE 1. Freshwater-age distributions in spawning ground samples, 1984–85. Percentages in parentheses.

Location	Date	Freshwater age				Total
		0.	1.	2.	3.	
Tahltan Lake (site 1)	July 22 – Aug. 22, 1984	0	71 (92)	6 (8)	0	77 (100)
	July 29 – Aug. 14, 1985	0	215 (97)	7 (3)	0	222 (100)
Christina Lake (site 3)	Sept. 4, 1984	0	31 (43)	41 (57)	0	72 (100)
Chutine Lake (site 2)	Sept. 4, 1984	0	45 (56)	34 (43)	1 (1)	80 (100)
	Sept. 12, 1985[a]	0	47 (46)	55 (54)	0	102 (100)
Chutine River (site 4)	Sept. 4, 1984	1 (2)	58 (95)	2 (3)	0	61 (100)
	Sept. 13, 1985[b]	5 (6)	71 (91)	1 (1)	1 (1)	78 (99)
Scud River (site 5)	Sept. 7, 1984	10 (23)	32 (73)	2 (5)	0	44 (101)
	Sept. 5, 1985	13 (20)	53 (80)	0	0	66 (100)
Stikine Mainstem:						
site 8	Sept. 5, 1985[c]	5 (21)	18 (75)	1 (4)	0	24 (100)
site 10	Sept. 4, 1985[c]	28 (55)	23 (45)	0	0	51 (100)
Iskut River:						
at Verrett River (site 6)	Sept. 10, 1984	3 (2)	133 (95)	4 (3)	0	140 (95)
	Aug. 10, 1985	17 (17)	82 (83)	0	0	99 (100)
	Sept. 8, 1985	12 (21)	38 (67)	7 (12)	0	57 (100)
site 7	Aug. 2 – 14, 1985	28 (17)	137 (81)	5 (3)	0	170 (101)

[a] Includes 57 fish aged with scales only.
[b] Includes 31 fish aged with scales only.
[c] Age determined from otoliths only.

Accordingly, we pooled data across years and sites to compute rough estimates of the relative occurrence of sea-type (15%) and river-type sockeye (85%) in river sites.

GROWTH RATES OF JUVENILE SOCKEYE

We monitored growth and dispersion of juvenile sockeye in the lower Stikine and Iskut rivers to test inferences about juvenile life history based on scale and otolith characteristics. Unfortunately, fyke nets set during late May and early June, 1985 in the main channel of the Iskut River (Fig. 2) and at the outlet of CHRL were not very effective. Only 2 (13%) age 1+ smolts were captured in the Iskut River before the net was destroyed by debris; the remainder of the juveniles captured (87%) did not have freshwater checks on their scales but many seemed too large (>46 mm fork length) to have emerged in the spring of 1985 (Fig. 3). Since these individuals were captured in a stationary net, opening upstream, it is probable that they were migrating sea-type sockeye with scale patterns corresponding to those observed among age 0. spawning adults. The juvenile samples from CHRL included a variety of ages: 0+ (6.5%), 1+ (54.4%), 2+ (34.8%), and 3+ (4.4%). The 3 age 0+ specimens were all relatively large (64–67 mm) and were probably yearling smolt with poorly developed checks. The smolts with typical 1+ circulus patterns averaged 72 mm (SD = 5.6) in length and 3.0 g (SD = 0.7) in weight; the age 2+ smolt averaged 81 mm (SD = 6.4) in length and 3.8 g (SD = 0.7) in weight. In contrast, a representative sample of 162 smolts from TAHL collected May 25–June 9, 1985 was 97.5% age 1+ averaging 77 mm (SD = 3.8) in length and 3.6 g (SD = 0.7) in weight; the age 2+ smolts averaged 106 mm (SD = 9.8) and 8.8 g (SD = 2.5) based on a larger sample (*n* = 18) representative of the 2+ cohort. A representative sample of 697 smolts collected from TAHL during May 6–July 7, 1984 was 89.1% age 1+ averaging 5.7 g, and 10.9% age 2+ averaging 10.5 g (S. Johnston, Department of Fisheries and Oceans, Whitehorse, Yukon, pers. comm.).

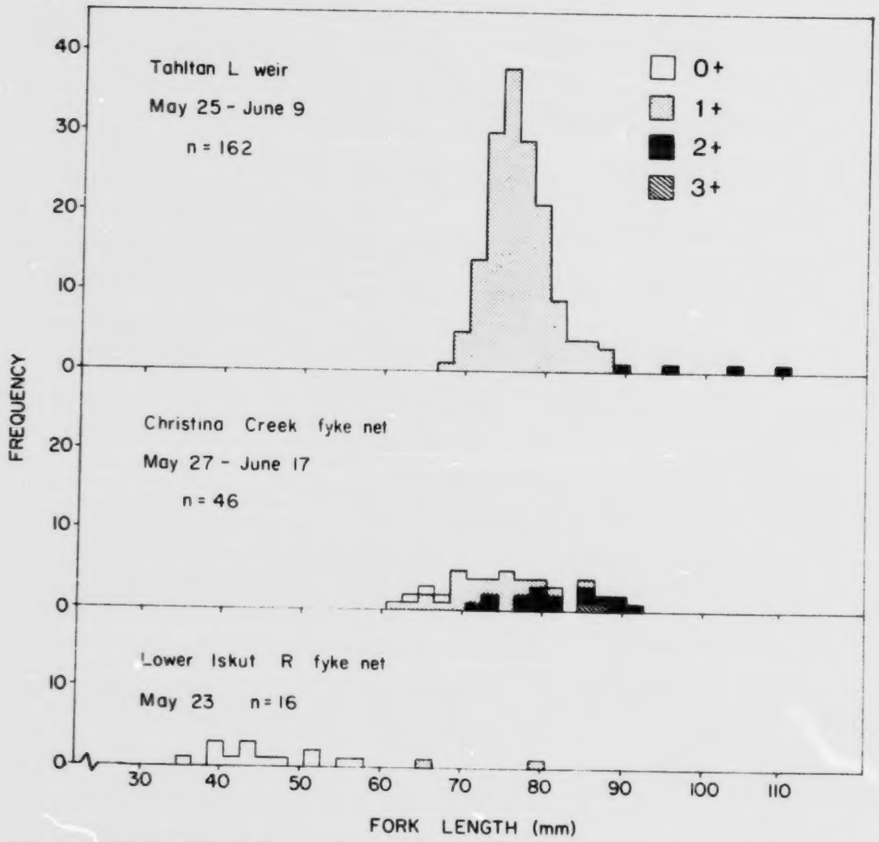

FIG. 3. Length distributions by age for juvenile sockeye captured in stationary traps in three different habitats during the smolt migration period, May 25–June 17, 1985.

Length distributions for juvenile sockeye collected from May 19 to Oct. 27 with beach seines in a slough in the lower Iskut River (site BS 3 in Fig. 2) are presented in Fig. 4. Age 1+ fish were captured on May 19 but not in subsequent sampling periods, which suggests that the smolt migration had finished prior to May 30. The large (>46 mm) age 0+ cohort, observed in the fyke net on May 23, comprised 50% of the May 19 beach seine sample but only 11% of the May 30 sample. This fact suggests, again, that these individuals were sea-type sockeye migrating downstream. The average weight of age 0+ fish in the combined fyke net and beach seine samples collected May 19–23 was 0.9 g (SD = 0.3, n = 49). The modal size of young-of-the-year sockeye shifted from 37 to 39 mm on May 30 to 49–50 mm by Oct 27. The fastest growth (assuming all observations pertain to a single cohort) occurred during August and September when water temperatures reached their maximum (approximately 9.5°C). Presumably the larger members of the cohort would attain lengths >60 mm characteristic of the age 1+ smolt captured on May 19, by late May 1986. It also seems likely that the smaller individuals (<50 mm) in the Oct. 27 sample would remain <60 mm by May 1986, and thus, may correspond to the large 0+ group in the May 19–23 samples. It is not known whether these small fry emerged very late in the summer or grew very slowly. Nevertheless, there is considerable variation in the size of young-of-the-year fish captured at sites within 10 km of the Iskut–Stikine confluence during a 2-wk period from Aug. 23 to Sept. 6, 1985 (Fig. 5). Fry collected at one site (BS 1) on Sept. 6 ranged from 29–75 mm; none showed freshwater checks on their scales. Fry collected along the margin of the main channel of the Stikine River (BS 5) were generally larger than those collected in slackwater areas. Water temperature ranged from 7.5 to 11.5°C among sampling sites in the river and was slightly higher (12°C) in Christina Lake.

IDENTIFICATION OF RIVER STOCKS IN FISHERY SAMPLES

Sockeye spawning at the river sites invariably had a greater chance of being infected by the brain parasite *Myxobolus neurobius* (Table 2). The parasite was generally absent from lake-type sockeye with the highest prevalence being only 10% (in CHRL, 1984). Prevalence among river stocks ranged from 13 to 15% in the Iskut River to 66% in the Scud River and 73% in one small sample from the Stikine mainstem. Furthermore, parasite prevalence was very consistent at all sites sampled repeatedly except Scud River, but those samples were not significantly different either ($P>0.05$, χ^2). The small sample from site 8 was, however, significantly different from the other mainstem Stikine sites ($P<0.001$, χ^2). Overall, the average parasite prevalence was 15% for the Iskut River sites, and 37% for all other river sites.

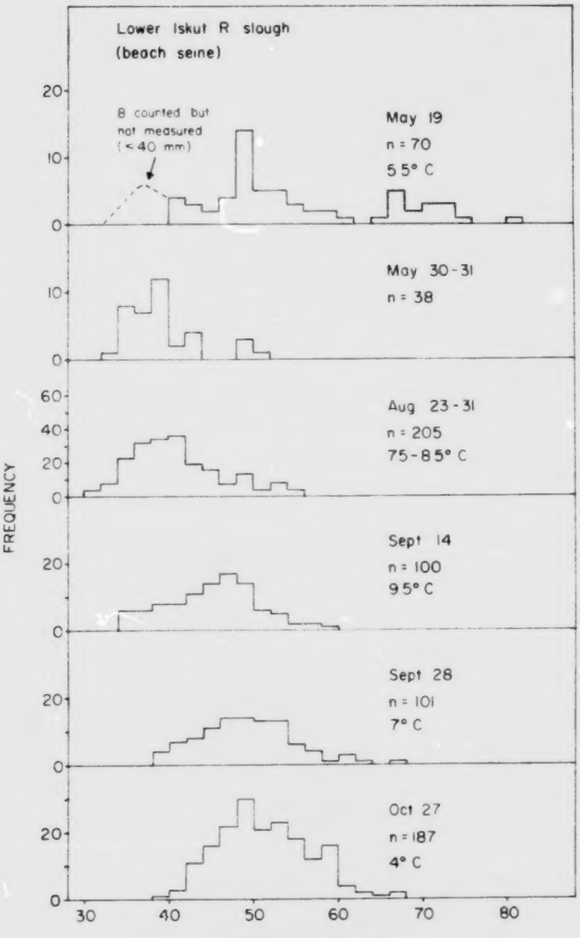

FIG. 4. Length distributions for juvenile sockeye captured by beach seine from a slackwater sidechannel in the lower Iskut River (BS 3 in Fig. 2). Stippled area represents juveniles with a freshwater check in scales; white area represents those without a freshwater check. Water temperature is indicated where available.

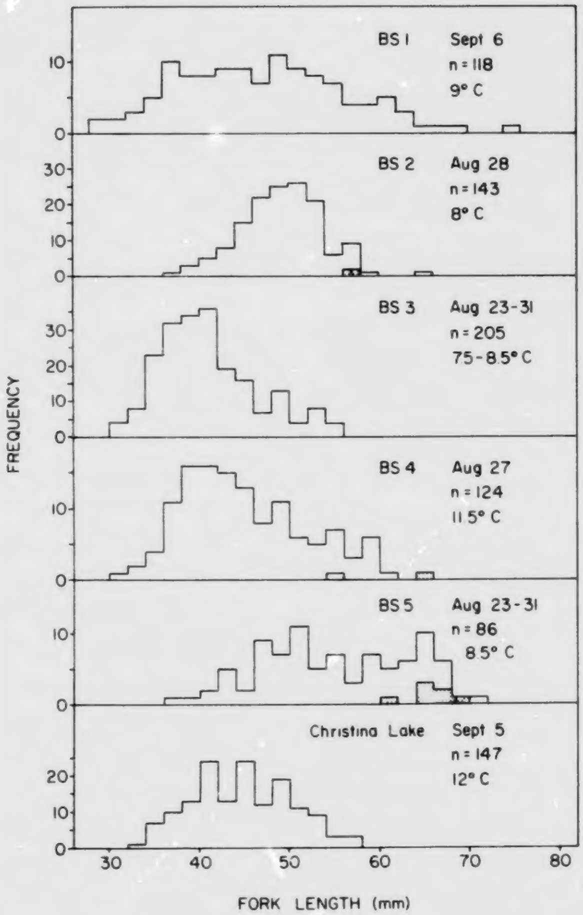

FIG. 5. Length distributions for juvenile sockeye captured by beach seine from five different locations within a 10 km radius of the Stikine-Iskut confluence and from Christina Lake. All samples were collected within a 2-wk period, Aug. 23–Sept. 6, 1985. Locations BS 1–BS 4 were slackwater sidechannels whereas BS 5 the margin of the main channel (see Fig. 2). Stippled area represents juveniles with a freshwater check in scales. Water temperature at each site is indicated.

There was some evidence to suggest that parasite prevalence was correlated with freshwater age. Prevalence among age 0. fish was 39 and 16% in pooled samples from the Stikine River (sites 4, 5, 8, 10) and the Iskut River (sites 6,7), respectively, compared with 55 and 23% for age 1. fish from the same samples. In the test fishery samples, parasite prevalence among age 0. fish was 31% (n = 13) and 27% (n = 30) in 1984 and 1985, respectively. Only 2% of fish sampled in the 1985 subsistance fishery at Telegraph Creek (site 11) were parasitized, which supports the conventional assumption that the fishery exploits, almost exclusively, sockeye destined for TAHL.

Electrophoretic analysis of eight polymorphic enzymes also revealed useful differences among samples from TAHL, CHUL and the other areas. The river stocks were very similar to each other at all loci (Fig. 6A). These data are reported in detail by Wood et al. (1987b).

Age 1.3 sockeye from TAHL typically formed more circuli during their first year of freshwater life (mean NC(1) = 12.30, SD = 1.61) than those from other areas (pooled NC(1) = 8.41, SD = 1.84). There were no significant differences in circuli counts for other growth zones. These data are also summarized in detail by Wood et al. (1987b).

The similarity dendrogram in Fig. 6B illustrates the combined discriminating power of all traits available from the 1985 test fishery samples, *viz.* freshwater age, parasite prevalence, and four electrophoretic traits. The stock composition of simulated mixtures of known composition was estimated using various subsets of discriminating traits (Table 3). Precision was improved substantially by summing allocations for the most similar stocks to provide estimates for three major groupings — TAHL, the glacial lakes, and the river

TABLE 2. Prevalence of the brain parasite, *Myxobolus neurobius*, by sample location, 1982–85.

Sample location	year	Number examined	Number infected	Proportion infected	± 95% C.I. (approx.)
Tahltan Lake	1982	30	0	0	—
	1983	100	0	0	—
	1985	99	1	0.01	0.02
Christina Lake	1984	50	5	0.10	0.09
	1985[a]	46	0	0	—
Chutine Lake	1984	100	9	0.09	0.06
	1985	50	2	0.04	0.06
Chutine River	1984	62	29	0.47	0.13
	1985	50	22	0.44	0.15
Scud River	1984	50	33	0.66	0.14
	1985	67	33	0.49	0.13
Stikine Mainstem;					
site 8	1985	22	16	0.73	0.21
site 9	1983	118	40	0.34	0.09
site 10	1985	53	15	0.28	0.13
all sites	—	193	71	0.37	0.07
Iskut River:					
at Verrett River	1983	110	17	0.15	0.07
	1984	151	23	0.15	0.06
	1985[b]	159	21	0.13	0.06
site 7	1985	177	26	0.15	0.06
all sites	—	597	87	0.15	0.03
Telegraph Creek (site 11)	1985	286	5	0.02	0.02

[a] Parasite prevalence tends to be underestimated by 5–10% in smolt samples.
[b] Aug. 10 and Sept. 8 samples combined.

TABLE 3. Stock composition estimates for mixtures of known composition. Mean proportions (± 1 SD) calculated by summing estimated proportions for each of six contributing stocks to give three principal stock-groupings for 100 simulated mixtures.

Details of the mixture analysis	Estimated Proportions		
	Tahltan Lake	Glacial lakes	River stocks
Actual composition	0.167	0.333	0.500
parasite, circuli counts[a]	0.167 (0.038)	0.258 (0.072)	0.575 (0.073)
parasite, total age circuli traits[a]	0.153 (0.036)	0.368 (0.048)	0.479 (0.050)
electrophoretic traits (4)	0.194 (0.040)	0.369 (0.123)	0.437 (0.146)
electrophoretic traits (4) parasite	0.188 (0.033)	0.322 (0.078)	0.489 (0.096)
electrophoretic traits (4) parasite, freshwater age	0.179 (0.027)	0.338 (0.050)	0.483 (0.054)
Actual composition	0.500	0.200	0.300
electrophoretic traits (4)	0.465 (0.072)	0.176 (0.101)	0.360 (0.116)
electrophoretic traits (4) parasite	0.473 (0.067)	0.186 (0.079)	0.341 (0.084)
electrophoretic traits (4) parasite, freshwater age	0.473 (0.065)	0.211 (0.059)	0.316 (0.051)

[a] Circuli counts from zones 1, 2, and 3 for age 1.3 only.

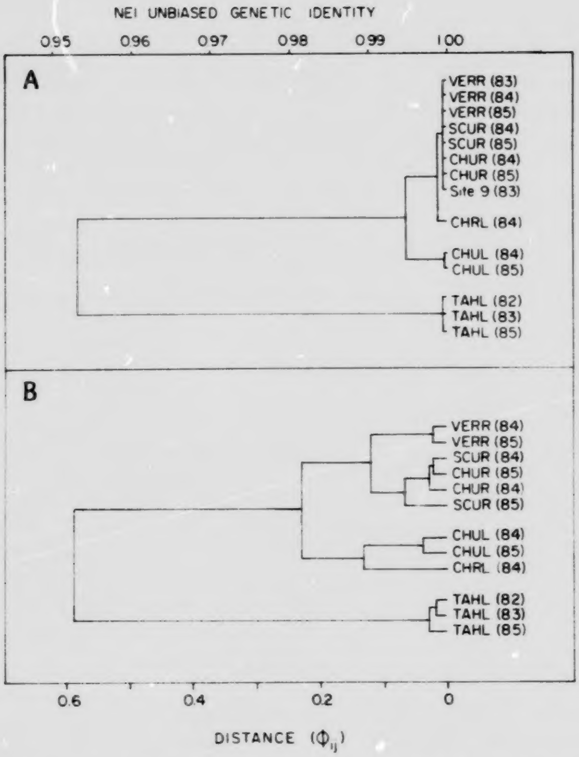

FIG. 6. Similarity dendrograms for samples of spawning sockeye collected from six principal spawning areas, 1983–85. A — dendrogram derived by the unweighted pair-group method using Nei's unbiased genetic identity (Nei 1978) and eight polymorphic loci. B — dendrogram derived using the modified Nei distance (equation [1] and 4 polymorphic loci, parasite prevalence and freshwater age. Samples from sites 6 and 9 in 1983 were not included because age data were not available.

stocks. As expected, the precision of the estimates increased as more traits were used, but in general, precision was very good.

Stock composition estimates for the test fisheries are summarized in Table 4. The estimated contribution from TAHL was similar in both years, accounting for 36 – 39% of the test fishery samples. The glacial lakes accounted for only 11 – 16% whereas the river stocks contributed 43% and 53% in 1984 and 1985, respectively. Estimates of composition by month indicate that the TAHL component predominates in the first half of the fishery; this confirms expectations based on run timing at the weir and tagging results (S. Johnston, Department of Fisheries and Oceans, Whitehorse, Yukon, pers. comm.) and is consistent with an alternative procedure for estimating the contribution from TAHL using egg diameter as an index of maturation (Craig 1985).

Egg diameter distributions from representative samples of the 1984 and 1985 test fisheries are presented in Fig. 7. Craig (1985) demonstrated that females destined for TAHL carry smaller eggs than sockeye from other stocks, and thus, account for the mode below 3.6 mm in the egg diameter distributions. Additional samples collected from several upstream locations in 1985 confirm his conclusions but reveal some overlap in the egg diameter distributions for TAHL and the lower Iskut River (Fig. 8). It is not known whether sockeye from TAHL possess smaller eggs at the time of spawning, because the eggs may continue to develop after the fish have passed through the weir and entered the lake.

Further corroboration of the egg diameter technique for stock identification was provided by estimating stock composition of test fishery samples with eggs <3.6 mm independently of those with eggs ≥ 3.6 mm using the mixture model and other traits (Table 5). The inferior separation of TAHL fish in 1984 is consistent with the position of the assumed threshold (3.6 mm) relative to the two modes in Fig. 7A; probably, a lower threshold would have provided

TABLE 4. Best estimates of stock composition from test fishery samples, 1984–85. Mean estimates (± 1 SD) calculated from 100 bootstrapped estimates.

			Estimated Proportions		
Year	Mixture description	Sample size	Tahltan lake	Glacial lakes	River stocks
1984[a]	Site A	248	0.370 (0.087)	0.158 (0.056)	0.472 (0.078)
	Site B	91	0.489 (0.114)	0.187 (0.115)	0.324 (0.085)
	Sites A + B	339	0.391 (0.061)	0.156 (0.061)	0.433 (0.059)
1985[b]	June	121	0.740 (0.067)	0.002 (0.005)	0.259 (0.067)
	July	314	0.487 (0.049)	0.094 (0.027)	0.419 (0.052)
	August	226	0.047 (0.027)	0.198 (0.048)	0.756 (0.054)
	Total	661	0.364 (0.028)	0.107 (0.022)	0.529 (0.034)

[a] Estimates based on parasite, total age, and circuli counts from age 1.3 fish [NC(1), NC(2), NC(3)].

[b] Estimates based on parasite, freshwater age, and four electrophoretic traits.

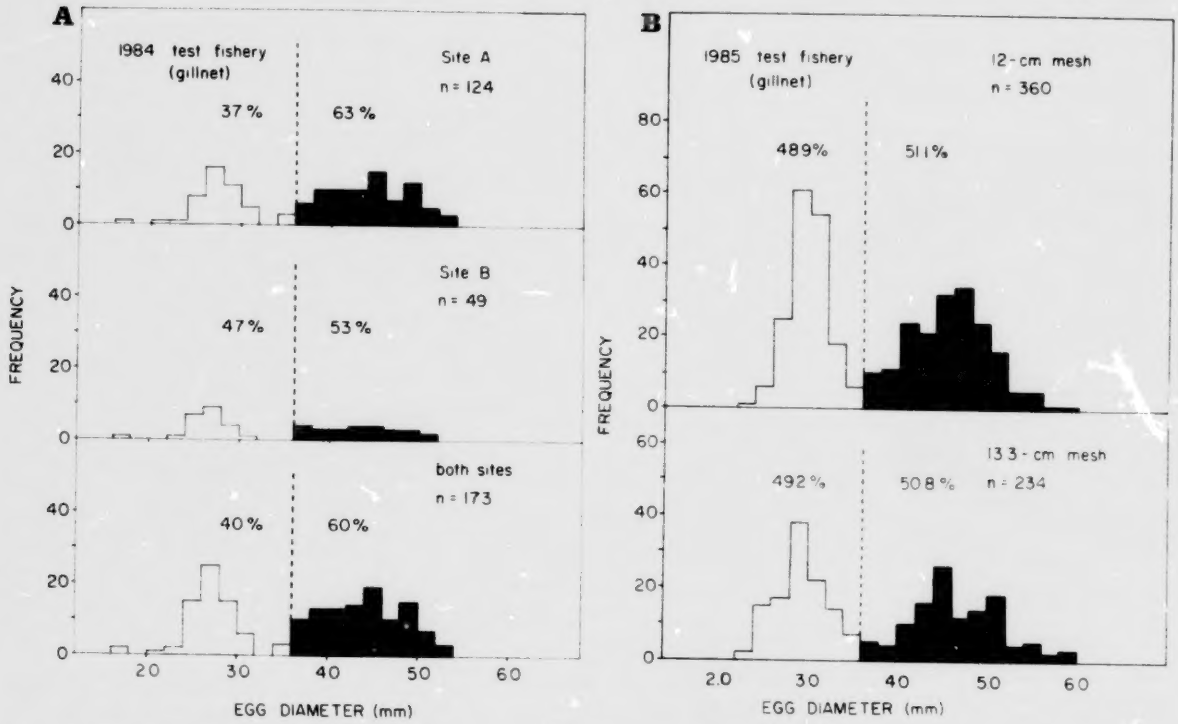

FIG. 7. (A) Egg diameter distributions in representative samples of female sockeye from the 1984 test fisheries in the lower Stikine River. Vertical dashed lines indicate the threshold used to determine contributions by Tahltan Lake and non-Tahltan Lake stocks (indicated by percentages); (B) Egg diameter distributions in representative samples of female sockeye from the 1985 test fisheries in the lower Stikine River. Vertical dashed lines correspond to those in Fig. 7A.

better resolution for the 1984 data. Nevertheless, the technique has obvious value for in-season monitoring of catch composition, and provides independent verification of the stock composition estimates in Table 4.

The mixture model and egg diameter methods provided very similar estimates for the TAHL contribution in 1984 (39 and 40%, respectively). After correction for misclassification rates given in Table 5, the final estimate from the egg diameter data was 38% TAHL. In 1985, the estimates were less similar owing to a biased sex ratio during the early part of the fishery. The TAHL contribution of female fish was estimated to be 41% using the mixture model compared to 49% using the egg diameter data (or 46% after correcting for misclassification). The TAHL contribution of male fish was estimated to be only 31% using the mixture model, resulting in an overall contribution of 36% for both sexes in aggregate.

ESTIMATION OF POPULATION SIZES

The absolute production by river stocks was estimated using stock composition estimates as indices of relative production in conjunction with information about the escapement to TAHL. It was also necessary to consider the catch by a food-fishery in Telegraph Creek (site 11) which is believed to exploit the run to TAHL. This assumption is justified because samples from the fishery were not significantly different ($P > 0.25$, χ^2) from those taken at TAHL with respect to the prevalence of the brain parasite, or electrophoretic characteristics at three loci. However, egg diameter and LDH-4 allele frequency data suggest that 10 – 20% of the catch at Telegraph Creek was contributed by another stock with large eggs (>4.2 mm), low parasite prevalence (6 – 11%), and LDH-4 allele frequencies typical of other river stocks (Wood et al. 1987b). The escapement to TAHL including 80% of the catch at Telegraph Creek as a conservative value, was 37 039 and 74 025 in 1984 and 1985, respectively (S. Johnston, Department of Fisheries and Oceans, Whitehorse, Yukon, pers. comm.). Thus, the total sockeye run escaping coastal fisheries in Southeast Alaska and the Canadian fishery in the lower Stikine River was approximately 95 000 (i.e., 37 039/0.39) in 1984 and 206 000 (i.e., 74 025/0.36) in 1985 using the estimates of contributions from TAHL in Table 4. Catches in the lower Stikine and in Alaskan waters must also be included to compute total production.

It follows that the escapement of river stocks would have been roughly 41 000 (43%) and 109 000 (53%) in 1984 and 1985, respectively. These escapements would have included 4400 and 9700 sea-type sockeye, based on estimated contributions to the test fishery samples of 4.6 and 4.7%, respectively. By subtraction, river-type sockeye accounted for about 36 600 (39%) and 99 000 (48%) of the 1984 and 1985 escapements. The remaining escapement, 56% in 1984 and 47% in 1985, represents the overall contribution by lake-type sockeye.

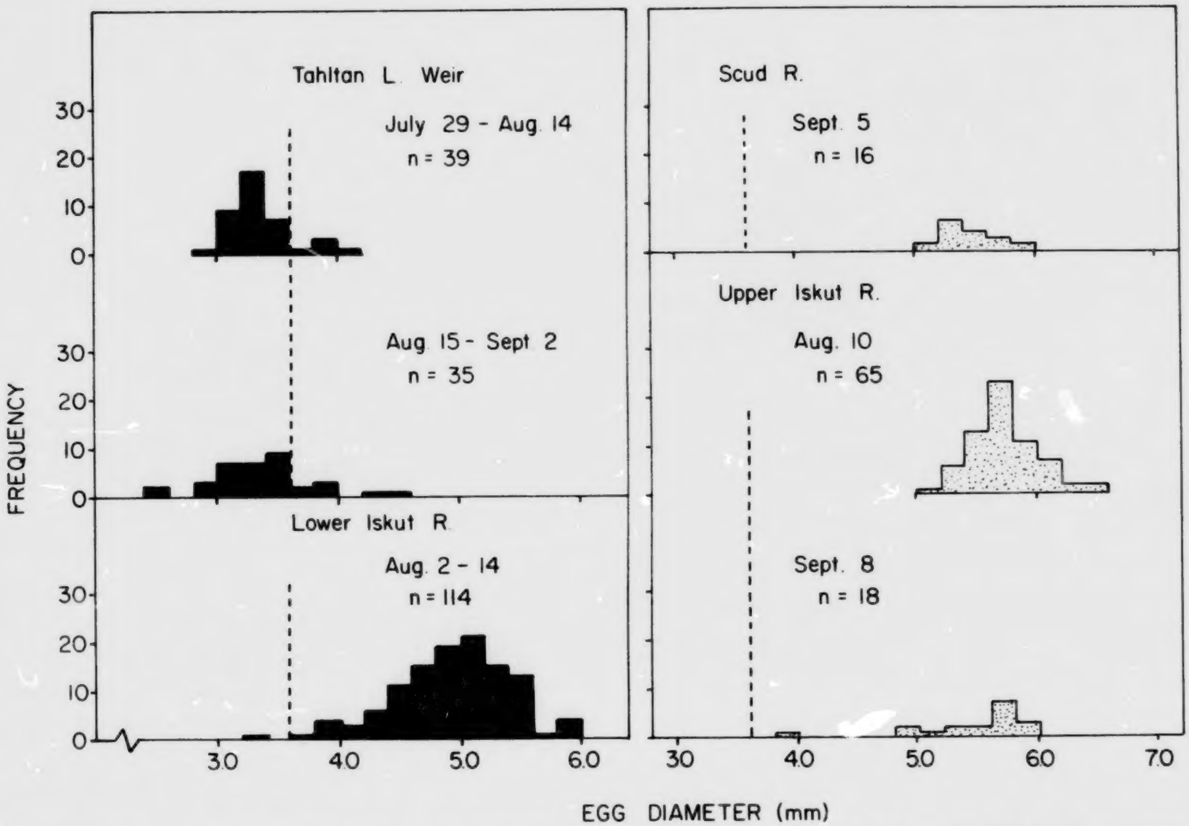

FIG. 8. Egg diameter distributions from sockeye collected in 1985 from locations upstream of the test fisheries. Black histograms represent samples collected during migration to spawning areas; stippled histograms represent samples collected on spawning grounds. Vertical dashed lines correspond to the stock separation threshold shown in Fig. 7.

TABLE 5. Best estimates of stock composition from test fishery samples, 1984–85, classified by egg diameter. Mean estimates (±1 SD) calculated from 100 bootstrapped estimates. Samples include all available data and are not weighted by catch rate.

			Estimated proportions		
Year	Mixture description	Sample size	Tahltan Lake	Glacial lakes	River stocks
1984[a]	small eggs (<3.6 mm)	129	0.728 (0.087)	0.190 (0.090)	0.083 (0.044)
	large eggs (≥3.6 mm)	189	0.149 (0.072)	0.195 (0.085)	0.657 (0.087)
1985[b]	small eggs	243	0.918 (0.082)	0.006 (0.041)	0.077 (0.047)
	large eggs	188	0.023 (0.029)	0.220 (0.058)	0.758 (0.072)

[a] Estimates based on parasite, total age, and circuli counts from age 1.3 fish [NC(1), NC(2), NC(3)].

[b] Estimates based on parasite, freshwater age, and four electrophoretic traits.

Discussion

The preceding analysis indicates that a major component of sockeye production in the Stikine River originates in habitat generally considered unsuitable for this species. Our conclusions rest on two premises: first, that the stock identification techniques are reliable, and second, that the test fishery samples were representative of sockeye populations in the Stikine River.

Samples from only three spawning areas (SCUR, CHUR, and VERR) were included in the mixture analysis to represent river stock contribution. We assumed that these samples were typical of other undiscovered spawning areas along the mainstems of the Stikine and Iskut rivers becauses they were very similar to each other (see Fig. 6). Stocks present in the test fishery sample, but not represented by a learning sample, would be misclassified to the most similar learning sample. Such misclassification would tend to underestimate rather than overestimate the contribution by river stocks since learning samples were available from all known lake stocks. The stability of the stock composition estimates using various subsets of traits suggests that no unique stock-groupings have been overlooked in the analysis. Furthermore, the estimated contribution from TAHL determines the population size estimates and TAHL is the most unique stock of those considered. The estimates for simulated mixtures of known composition (Table 3) demonstrate that TAHL is accurately determined using a variety of traits.

It is more difficult to determine whether the test fishery samples are truly representative of the entire sockeye run. The selective effect of mesh size can be discounted as a significant source of bias; samples collected with a 12-cm mesh gillnet showed no obvious differences from those collected with a 13.3-cm mesh net with respect to length distribution, sex ratio, parasite prevalence, or egg diameter distribution. Catchability may have changed slightly owing to the rise and fall of river level over the period of upstream migration. Overall, the river level dropped by 3.7 m (25% of the maximum depth at the site) between July 5 and August 29, 1985. This may have increased the catchability of the river stocks relative to the earlier-migrating TAHL component. Stocks with lower catchability would be underrepresented in the sample.

The river is very wide (200–400 m) at the test fishery sites so that only a small fraction of the total cross-sectional area adjacent to a river bank can be sampled with fixed gillnets. Thus, any differences in migratory behaviour among stocks might have resulted in biased samples. However, all estimates of the TAHL contribution based on several different variables and on samples collected at three different locations, and in two different years, fell within the range of 36–49%. The locations considered a priori to give the most representative samples — site A in 1984 and the site used in 1985, provided estimates of 39 and 36% TAHL, respectively.

The proportion of female sockeye in the 1985 test fishery samples increased form 50% on June 11 to 71% on July 7 towards the end of the TAHL run, then stabilized at 50–55% from July 27 to Aug. 30 during the migration of the river stocks. A similar pattern was observed in 1983 (Craig 1985). This trend accounts for differences in the stock composition estimates by sex, with TAHL comprising 41% of the female catch but only 31% of the male catch. However, the sex ratio at the TAHL weir was only 44% female. It is possible that due to obstacles in the river TAHL females suffered higher mortality than TAHL males during the upstream migration (Ricker 1987), but this seems unlikely because males and females were equally represented in catches of the food-fishery at Telegraph Creek. More probably, the unequal sex ratio in the test fishery samples reflects a sampling bias. The bias cannot be attributed to size-selectivity because similar sex ratios were obtained in both the 12-cm and 13.3-cm mesh nets, and there were no large differences in the size of spawners among stocks. Unfortunately, it is not clear whether TAHL females were oversampled relative to river stock females, or whether TAHL males were undersampled relative to the river stock males. In the former case, the male catch would provide an unbiased estimate, whereas in the latter case the female catch would be more representative.

Sequential samples of juvenile salmon captured in the lower Stikine and Iskut rivers demonstrate that juvenile sockeye rear in a wide variety of river channel and slough habitats for extended periods. In general, the larger individuals inhabited the margins of the main channels where the current was weak, whereas smaller individuals tended to occur in slackwater areas. The distinction between sea-type and river-type sockeye in this paper refers only to the presence or absence of a fresh water annulus. The juvenile length distributions in Fig. 3–5 suggest that at least some sea-type sockeye spend many months, if not the majority of the growing season, in fresh water. Further study is required to determine whether the observed heterogeneity in size among underyearlings is caused by variation in time of emergence and growth rate within spawning groups associated with heterogeneous temperature regimes, or results from intermingling of juveniles from many different spawining groups during a prolonged downstream migration.

The magnitude of sockeye production from riverine and glacial lake habitats within the Stikine River watershed was not recognized until recently because of difficulties in enumerating, directly, spawning populations that are sparsely distributed in turbid water throughout remote areas. Advances in statistical techniques for stock identification that allow the use of a variety of biological markers simultaneously, make it feasible to assess the contribution of such stocks, indirectly, through test fisheries. Total escapement to the Canadian portion of the Stikine River ("border escapement") has been estimated using indirect methods since 1982. The methodology has evolved from the use of scale pattern analysis to identify Tahltan Lake sockeye in samples from the in-river commercial catch, to the use of five types of discriminating characteristics to identify relative contributions by three major stock-groupings in catches from test fisheries designed to obtain a representative sample over the entire sockeye run.

The earlier hypothesis that Tahltan Lake produces 90% of sockeye from the Stikine River (Bergmann 1978) is no longer tenable. Non-Tahltan spawning stocks have accounted for the majority (52–64%) of sockeye production in the Stikine River since 1982 (this study; Craig 1985). River-type and sea-type sockeye accounted for over 70% of the non-Tahltan production in 1984 and 1985; their importance in previous years has not been assessed. It is also noteworthy that the estimated contribution from Tahltan Lake has varied narrowly between 36 and 44% since 1982 despite a threefold variation in border escapement. Although the rearing environments within the watershed differ dramatically, the relative productivity of each habitat appears to have remained relatively constant. This suggests that the fluctuations in border escapement were not caused by freshwater events.

The difficulty of enumerating spawning salmon populations in watersheds like the Stikine River severely limits our ability to manage these fishery resources. Procedures outlined in this paper offer much promise for improving escapement estimates where other techniques are impractical. Indeed, it seems probable that further application of these techniques will reveal substantial production by river-type sockeye in other northern rivers, such as the Taku River, which possess extensive slackwater habitat for rearing and sufficient upwelling groundwater for successful spawning.

Acknowledgements

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Underyearling Sockeye Salmon (*Oncorhynchus nerka*) in the Estuary of the Fraser River

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Abstract

BIRTWELL, I. K., M. D. NASSICHUK, AND H. BEUNE. 1987. Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River, p. 25-35. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Underyearling sockeye salmon were the most abundant salmonid, and the fifth most abundant fish species captured during an 18-month study in Deas Slough (2.7 × 0.25 km × 5 m depth), 10 km upstream from the mouth of the Fraser River. Catches of these underyearlings were significantly ($P<0.05$) larger in the upper slough area when compared to those at sites closer to, and in, the main Fraser River channels. Similarly, condition factors were also higher for those captured in the upper slough habitat. Underyearlings were present in the slough for approximately 5 months. They were most abundant in late June and early July. In contrast, very low numbers of age 1^+ sockeye utilized the same areas, and they were only present for a 6-wk period (April–June). The size of underyearling sockeye captured in Deas Slough increased rapidly and in early autumn their lengths were equivalent to those of some of the spring, age 1^+, downstream migrants (65–75 mm). Primary prey of underyearlings in the several habitats examined were: cladocerans and copepods, in the upper slough; oligochaetes, copepods, and insects in the lower slough; and insects in the river channels. Overall, the data strongly suggest that populations of underyearling sockeye salmon rear successfully in the Fraser River estuary. This life history pattern contrasts with that of the majority of sockeye salmon in the watershed, which rear in freshwater lakes for about 1 yr before migration to sea.

Résumé

BIRTWELL, I. K., M. D. NASSICHUK, AND H. BEUNE. 1987. Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River, p. 25-35. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Le saumon nerka de moins d'un an représentait, par ordre d'importance, le premier salmonidé et la cinquième espèce capturés au cours d'une étude de 18 mois menée dans le marais Deas (2,7 × 0,25 km × 5 m de profondeur) situé à 10 km en amont de l'embouchure du fleuve Fraser. Les prises de saumons de moins d'un an étaient nettement plus élevées ($P<0,05$) dans la partie supérieure du marais qu'aux autres endroits situés dans la partie principale du fleuve Fraser ou à proximité. Il en était de même pour les facteurs de condition qui étaient plus élevés chez les salmonidés capturés dans la partie supérieure du marais. Les saumons de moins d'un an étaient présents pendant environ 5 mois dans le marais où ils étaient plus abondants à la fin de juin et au début de juillet. Par contre, un faible nombre de saumons nerkas de 1^+ an utilisaient les mêmes régions où ils n'étaient présents que pendant 6 semaines (avril–juin). La taille des saumons nerkas de moins d'un an capturés dans le marais Deas a rapidement augmenté; au début de l'automne, leur taille était semblable à certains migrateurs de printemps âgés de 1^+ retrouvés en aval (65–75 mm). Dans les habitats étudiés, les saumons de moins d'un an se nourrissaient surtout de cladocères et de copépodes dans la partie supérieure du marais, d'oligochètes, de copépodes et d'insectes dans la partie inférieure et d'insectes dans la partie principale du fleuve. En général, les données portent fortement à croire que l'estuaire du Fraser constitue un habitat propice à la croissance des populations de saumon nerka de moins d'un an. Ce différent cycle vital tranche sur celui de la plupart des populations de saumon nerka peuplant le bassin versant, qui fréquentent les lacs d'eau douce pendant environ un an avant de gagner la mer.

Introduction

Sockeye salmon (*Oncorhynchus nerka*) comprise about 50% of the Fraser River salmon fishery and they occur in all but one of the subbasins of the extensive (233 000 km^2) watershed. Their typical life cycle incorporates at least one year's residency in a freshwater lake before migration to sea in the spring (Foerster 1968; Northcote 1974). There is little information on the use of lower Fraser River and estuarine areas by sockeye salmon (Northcote 1974). Within the Fraser River system large numbers of age 1$^+$ sockeye migrate seaward in the spring. The majority of them occur in the faster flowing, mid-channel regions of the river and leave the estuary rapidly (Goodman 1975; Beak Consultants Ltd. 1981). Their temporary presence has, however, been recorded in shallow regions of the inner estuary, within 20 km of the Fraser River mouth (Northcote 1974; Dunford 1975; Goodman 1975; Anderson et al. 1981; Levy and Northcote 1981, 1982). Similarly, extremely low numbers of age 1$^+$ sockeye occupy, for very brief periods, the outer estuarine areas of Roberts and Sturgeon Banks (Greer et al. 1980; Gordon and Levings 1984; Macdonald 1984; Mesa 1984).

Contrasting with this typical life history pattern is that of a population of sockeye salmon which does not appear to reside in a freshwater lake for one year, and migrates to sea as underyearlings (Gilbert 1918; Foerster 1968; Northcote 1974). The adults of this population are considered to spawn on gravel bars in a shallow backwater region near the Harrison rapids, about 100 km from the mouth of the Fraser River. Recent studies have revealed the presence of underyearling sockeye in estuarine habitats of the Fraser River (Dunford 1975; Levy and Northcote 1982; Macdonald 1984). While this life history pattern is exceptional in the Fraser River sockeye, no specific research has been carried out to examine the status of these fish, nor the ecology of the juveniles.

This report describes aspects of the ecology of juvenile sockeye salmon in Deas Slough, a permanently wetted, tidally influenced backwater area, 10 km from the mouth of the Fraser River, and in adjacent estuarine areas.

Materials and Methods

LOCATION

Sampling sites were selected as part of an investigation to examine the likely effects of proposed river training walls on fish populations. Deas Slough (approximately 2.7 × 0.25 km × 5 m depth), which was formerly a side arm of the Fraser River, was dammed at its upstream end in 1948, thus creating the slough which opens to Ladner Reach, a large side channel from the main south arm of the Fraser River (Fig. 1). Deas Slough contains two large marinas and is also used for log storage.

For comparative purposes, 12 sampling sites were grouped to represent three areas (4 sites per area): upper Deas Slough, lower Deas Slough, and an open channel environment — Ladner Reach and Woodward Reach (Fig. 1).

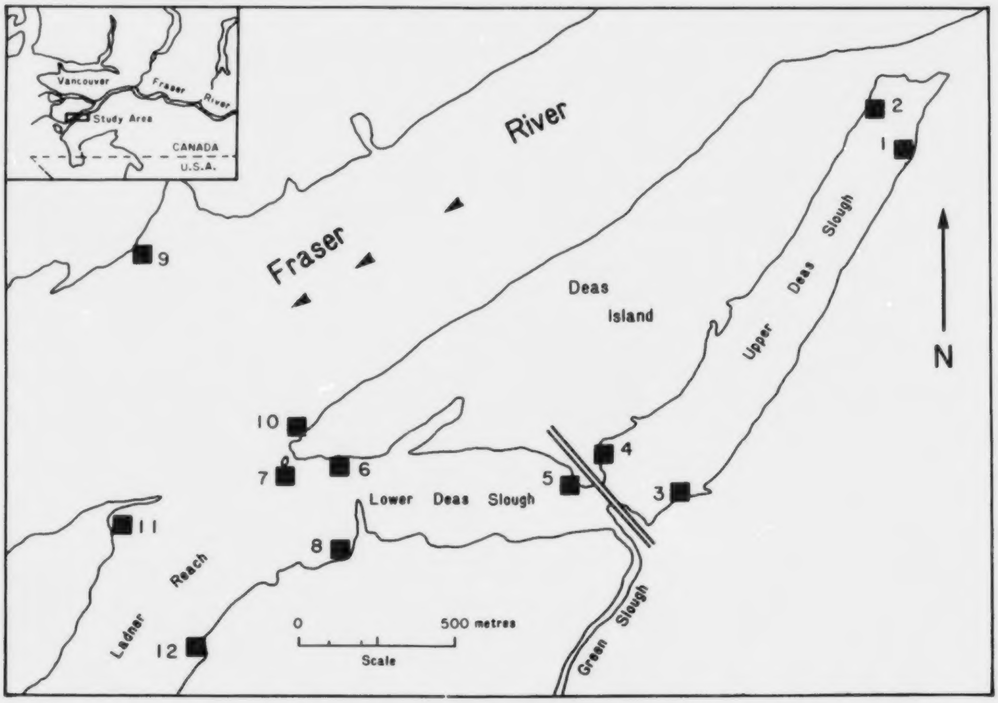

FIG. 1. The location of sampling sites in the Deas Slough—Leadner Reach region of the Fraser River estuary: upper Deas Slough — sites 1 to 4; lower Deas Slough — sites 5 to 8; Ladner Reach — sites 9 to 12.

FISH CAPTURE AND TREATMENT

A beach seine (30 × 2 m) was deployed from a shallow draft boat at each of the sampling sites. It was estimated that the net probably fished an area of about 200 m^2 and a volume of about 300 m^3. Sampling was carried out during daylight and standardized with respect to tidal height. The main sampling program was at high tide (3.2 ± 0.6 m), biweekly from August 1976 to October 1977, but once a month October to February, and at low tide (less than 2.8m) August to November 1976.

Samples of fish were either killed and preserved in dilute (10%) buffered formalin or anaesthetized (2-phenoxyethanol, quinaldine) (Bell 1964), identified, enumerated, and then released after length and weight determination.

The age of juvenile sockeye salmon was determined by scale analysis; a marked size difference was apparent between age 0^+ and 1^+ fish.

STOMACH CONTENTS ANALYSIS

Analyses of stomach contents followed the procedures described by Kask and Parker (1974), after transferring samples from buffered formalin to isopropyl alcohol (35%). Stomachs were removed, blotted dry, and weighed full and empty (± 0.001 g).

The volume of digested and unidentifiable constituents were estimated and recorded as a percentage of total contents. All prey items were measured (± 1.0 mm) and grouped into size categories in millimetre increments of total length. Size of prey items was determined for each stomach sampled. The percent compostition by number (the number of food items of a given species in a given subsample) was expressed as a percentage of all prey species, thus providing an estimate of the relative abundance of each prey species in the diet. The percent frequency of occurence of a prey item (the number of stomachs in which one or more of a given prey was found) was expressed as a percentage of all stomachs examined which contained prey.

Biomass values were derived from conversion data of Kask and Parker (1974), and information provided by the Provincial Government's Marine Resources Branch (E. Oguss, pers. comm.). Biomass values (the total biomass of a given prey species in all stomachs sampled) were expressed as a percentage of the total biomass of all prey species in the sample.

The relative importance of each prey item was determined and expressed as an index of relative importance (Pinkas et al. 1971).

WATER CHARACTERISTICS

At each sampling site, and on each occasion, temperature, dissolved oxygen, pH, oxidation-reduction potential and conductivity were measured at 0.5 m depth (using a Hydrolab Corporation Model 6D multiprobe sensing unit), in addition to Secchi disc (20 cm diameter) readings.

TABLE 1. Mean number of juvenile sockeye (*O. nerka*) salmon captured per beach seine ($n = 4$) in three locations of the Fraser River estuary. Values in brackets are for age 1^+ fish.

Sampling date	upper Deas Slough	lower Deas Slough	Ladner Reach
Aug. 2, 1976	0.25	1.50	5.67
*Aug. 9	3.00	0.67	
Aug. 16	17.50		0.50
*Aug. 23	28.67	3.67	
Aug. 30	9.00	1.75	
*Sep. 6		1.33	0.67
Sep. 13	8.50	1.25	
*Sep. 20	3.50		
Sep. 27	0.25		
*Oct. 4	0.67		
Oct. 11			
Nov. 8			
*Nov. 15			
Dec. 6			
Jan. 10, 1977			
Feb. 7			
Feb. 28			
Mar. 14			
Mar. 28			
Apr. 11			
Apr. 25	0.50 (0.50)	(0.25)	0.25 (0.25)
May. 9	2.00 (0.25)	0.50 (0.75)	0.25 (1.25)
May. 23	6.75	1.25	1.00
June 6	11.50 (0.50)	0.75	1.00
June 20	54.00 (2.00)	2.75	2.00
July 4	99.25	12.75	1.25
July 18	0.25	0.50	
Aug. 1		0.25	
Aug. 15			
Aug. 29	0.50	0.25	
Sep. 12			
Oct. 3			

* Low tide sampling; 3 sets per zone.

DATA ANALYSIS

Statistical analyses applied to transformed ($\mathrm{Log}_{10}\ n + 1$) catch data and to water characteristic information were: correlation anaysis, Students' test, Analysis of Variance, Duncan's Multiple Range Test (Steele and Torrie 1960; Sokal and Rohlf 1969). Fulton's condition factor (Ricker 1975) was calculated from weight and length measurements, as was the weight-length regression equation for fish collected from the three sampling zones; an Analysis of Covariance, *F*-test (Rao 1970) was used to establish if regression equations were similar for fish collected in those zones. A runs test (Siegel 1956) was used to examine fish-water characteristics interactions.

Results

DISTRIBUTION, UTILIZATION, AND ABUNDANCE

Sockeye salmon underyearlings were captured until October 1976, and in 1977 between April and August (Table 1). Their maximum abundance was in late June and early July, and catches in upper Deas Slough were significantly ($P<0.05$) greater (based on 42 seine sets) from this zone when compared to catches in lower Deas Slough and Ladner Reach. Although higher numbers were caught at high tide than at low tide, the difference was not statistically significant.

In relation to the other 23 species of fish captured by beach seine in this area, underyearling sockeye were ranked 5th, 9th, and 11th most abundant in upper Deas Slough, lower Deas Slough and Ladner reach zones, respectively. Furthermore, they had relatively high frequencies of occurrence at 26%, 21%, and 17%, and were present for 21.5, 17, and 13.5 wk in the respective zones.

Contrasting with catches of underyearling sockeye in the study area is the extremely low catch of age 1^+ sockeye. These age 1^+ fish were present between late April and early June in 1977 and probably reached maximum abundance a month earlier than underyearlings. They had a low frequency of occurrence ($<3\%$) and comprised less than 3% of the catches in the three sampling zones. Catches between zones were not significantly different from each other. The maximum annual utilization period by age 1^+ sockeye juveniles in this area was 6 wk in upper Deas Slough and 4 wk in the other two zones that were sampled.

Using catch per unit of area information at the time of maximum abundance, we can derive a very approximate value for the number of fish present along the shoreline. These areas (4.95 ha) extended 12.5 m from shore (equivalent to the distance the beach seines were set from the shoreline), and around the periphery of Deas Slough. Upper and lower Deas Slough were of approximately equal size; the 4.95 ha zone is equivalent to 13.3% and 15.7% of the surface area of upper and lower Deas Slough, respectively. The numbers of underyearling sockeye within the 4.95 ha zones were calculated to be 24 500 (June, upper Deas Slough), 3 100 (July, lower Deas Slough), and 500 (June, Ladner Reach, equivalent area). For age 1^+ sockeye, the values were 100 (April/June, upper Deas Slough) and 200 (May, lower Deas Slough and Ladner Reach).

The size of underyearling sockeye captured in the study area changed over time and by late summer was equivalent to that of spring-migrating age 1^+ fish (Fig. 2). Scale analyses revealed that underyearling sockeye predominated in the catches (Fig. 3). All were found to be age 0^+ in 1976 samples, whereas both age 0^+ and 1^+ fish occurred in 1977, the latter not being captured after June.

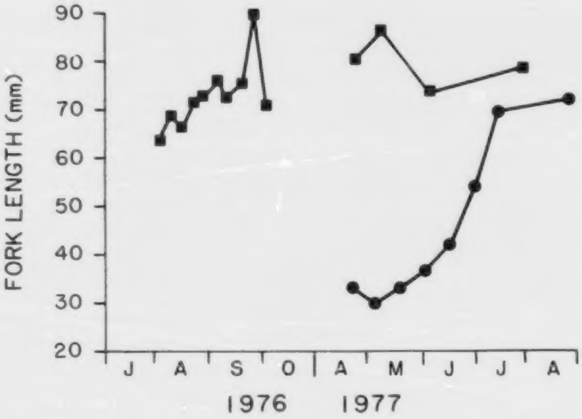

FIG. 2. Changes in the mean length of underyearling sockeye salmon determined from samples collected in the Deas Slough-Ladner Reach area of the Fraser River estuary: 1976 year-class — squares; 1977 year-class — dots.

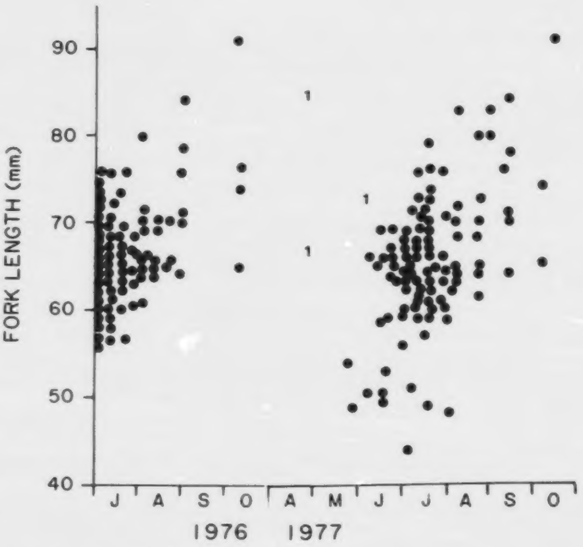

FIG. 3. Age-length relationship for samples of sockeye salmon collected in 1976 and 1977 from the Deas Slough-Ladner Reach area of the Fraser River estuary: age 0^+ — dots; age 1^+ — 1.

CONDITION FACTORS AND WEIGHT–LENGTH RELATIONSHIPS

Both underyearlings and age 1^+ sockeye captured from Deas Slough had greater condition factors than those fish captured in the Ladner Reach zone. Those condition factors for underyearling fish from Deas Slough (upper — 1.06, $n=132$; lower — 1.10, $n=59$) were significantly ($P<0.05$) greater than those from Ladner Reach (0.93, $n=23$).

Analysis of Covariance applied to weight–length data revealed no significant ($P<0.05$) difference between the relationships for underyearlings captured in the two zones of Deas Slough, but there was a difference between the regression data for fish from these zones and those from Ladner Reach. The common regression equation for underyearling sockeye from Deas Slough was $\log W = -5.29 + 3.21 \log L$, and that for Ladner Reach was $\log W = -5.80 + 3.51 \log L$; where W = weight (g) and L = length (mm).

Thus, fry up to 50 mm length weighed slightly more, per unit of length, in Deas Slough than in Ladner Reach, whereas the reverse pertained for fish greater than 50 mm in length. The common weight–length regression equation for yearling (1^+) sockeye from the study area was $\log W = -4.58 + 2.78 \log L$.

WATER CHARACTERISTICS AND SOCKEYE PRESENCE

Water characteristics data for the three zones in the study area, during the fish sampling program, were subjected to Analysis of Variance and Duncan's Multiple Range Test. The results of these analyses are presented in Table 2. Similar data are provided in Table 3, wherein the range, mean ± SD for particular variables are listed in relation to the presence of juvenile sockeye salmon. These data not only serve to characterize some of the aquatic conditons but also indicate the range of conditions in the estuarine habitats used by these fish.

Although data analysis did not reveal a significant ($P<0.05$) separation between temperatures in the three sampling zones over the duration of the study, temperatures in upper Deas Slough were generally warmer (by 4°C) than those in Ladner Reach during summer 1976, possibly reflecting differences in tidal and river flushing action.

Sockeye underyearlings occurred, on most occasions, in waters where the temperature was above the mean for the area, and ranged between 11.3°C and 20.4°C. No sockeye were captured when the maximum temperature (23°C) was recorded at a sampling site in upper Deas Slough (mid-August 1977).

TABLE 2. Results of Analysis of Variance and Duncan's Multiple Range Test applied to water characteristics information collected at 12 sites in 3 zones (A, B, and C) during the fish capture program in the Deas Slough–Ladner Reach region of the Fraser River estuary.

		Deas Slough		Ladner Reach (C)	Homogeneous data sets
		upper (A)	lower (B)		
Temperature (°C)	n	90	92	92	
$\bar{x} \pm SD$		13.7 ± 5.5	12.5 ± 5.1	12.1 ± 5.0	(C, B, A)
range		1.2 to 23.0	1.3 to 21.4	1.4 to 20.2	
Salinity (‰)	n	86	90	92	
$\bar{x} \pm SD$		0.2 ± 0.2	0.3 ± 0.6	0.4 ± 1.0	(A, B, C)
range		<0.1 to 1.0	<0.1 to 3.3	<0.1 to 5.9	
Dissolved oxygen (mg•L^{-1})	n	86	90	92	
$\bar{x} \pm SD$		10.1 ± 1.7	11.0 ± 1.0	11.4 ± 1.4	A–(B, C)
(% air saturation)	n	86	90	92	
$\bar{x} \pm SD$		99 ± 14	105 ± 6	108 ± 4	A–B–C
range		69 to 143	84 to 119	94 to 165	
pH	n	89	90	91	
$\bar{x} \pm SD$		7.4 ± 0.3	7.5 ± 0.3	7.7 ± 0.3	A–B–C
range		6.7 to 8.2	6.4 to 8.1	6.7 to 8.2	
Oxidation -reduction potential (meV)	n	89	92	92	
$\bar{x} \pm SD$		+263 ± 64	+267 ± 51	+270 ± 57	(A, B, C)
range		+90 to +360	+75 to +340	+40 to +350	
Secchi disc visibility (cm)	n	88	88	88	
$\bar{x} \pm SD$		62 ± 21	45 ± 17	44 ± 18	(C, B)–A
range		27 to 88	13 to 92	17 to 83	

TABLE 3. Water characteristics, determined at 0.5 m depth, when juvenile (age 0^+ and 1^+) sockeye salmon were captured in the Deas Slough–Ladner Reach area of the Fraser River estuary.

			Age 0^+	Age 1^+
Temperature	(°C)	n	72	9
$\bar{x}$ ± SD			15.7 ± 2.0	13.0 ± 2.7
range			11.3 to 20.4	10.4 to 17.4
Salinity	(‰)	n	69	9
$\bar{x}$ ± SD			0.1 ± 0.03	0.1 ± 0.03
range			<0.1 to 0.3	0.1 to 0.2
Dissolved oxygen	($\mathrm{mg \cdot L^{-1}}$)	n	69	9
$\bar{x}$ ± SD			10.2 ± 1.3	11.2 ± 1.1
range			8.7 to 15.8	9.5 to 12.9
	(% of air saturation)	n	69	9
$\bar{x}$ ± SD			106 ± 12.9	110 ± 5.6
range			77 to 165	102 to 119
pH		n	72	9
$\bar{x}$ ± SD			7.5 ± 0.4	7.2 ± 0.4
range			6.4 to 8.1	6.4 to 8.0
Oxidation–reduction potential	(mV)	n	72	9
$\bar{x}$ ± SD			+275 ± 36.5	+256 ± 50.1
range			+205 to +358	+143 to +316
Secchi disc visibility	(cm)	n	62	9
$\bar{x}$ ± SD			47 ± 23	41 ± 19
range			21 to 88	17 to 83

Salinities were highest in the study area during the winter low freshwater-flow period, when salt water intrusion into the estuary was greater than during spring and summertime. Lower salinity values were recorded at upper Deas Slough, while those at the more seaward Ladner Reach zone were marginally but not significantly higher (maximum values were substantially different, Table 2). In general, sockeye salmon underyearlings were present in the area when Fraser River freshwater flows were high (i.e. freshet). Accordingly, salinity values at the time of fish capture were correspondingly low and ranged from 0.1 to 0.3‰.

Sockeye fry were generally captured at sites with above average (for the study area) dissolved oxygen values. Higher numbers of fry occurred, however, in upper Deas Slough, whereas higher dissolved oxygen levels were typically recorded in Ladner Reach. Although mean values of dissolved oxygen (% of air saturation) were at, or just above, saturation (0.5 m depth), greater reductions (to 69% of air saturation) were recorded in upper Deas Slough. The reductions were, perhaps, a consequence of reduced flushing action relative to that in the Ladner Reach area. The minimum values of dissolved oxygen in surface waters were recorded in November 1976, when juvenile sockeye were no longer captured in the study area.

Sockeye fry occurred in waters with a wide range of pH. Mean values in the respective zones were separated statistically, but there was no correlation with fish presence.

Lower oxidation–reduction potential values were recorded in winter, but, when fry were present, they tended to inhabit waters with higher values.

Water clarity, as determined by Secchi disc readings, was typically greatest during winter and minimal during the freshet high turbidity conditions, which occur in the spring. Water clarity was significantly greater in upper Deas Slough than in either lower Deas Slough or Ladner Reach. Fry, when present, were associated with waters of variable but greater clarity than the average for the study area.

DIET

A total of 174 stomachs were examined from sockeye juveniles captured in the study area. While 44 prey items were identified, only 15 were major components.

Table 4 displays information on the prey items (biomass and frequency of occurrence) consumed by juvenile sockeye salmon between May and September 1977, together with those ranked first and second in relative importance. The types of prey items consumed by these fish throughout the study and their relative biomass (%) are presented in Table 5.

In upper Deas Slough, copepods (*Cyclops* sp.) and insects (chironomid larvae and pupae) were the important prey items in May and, while these insects were still major dietary constituents in June and July, cladocerans (*Daphnia* sp., *Bosmina* sp.) became of greater relative importance. Only two fish were analyzed in September from this location, and the cladoceran *Sida crystallina* was found to predominate in the diet.

Contrasting with these findings was the diet of underyearling sockeye in lower Deas Slough where, in May, oligochaetes were a major prey item. Insects were major prey items May to September (larvae and pupae). Oligochaetes were also a major component in June, but did not feature in the diet thereafter. Copepods (*Cyclops* sp.) were consumed in greatest quantities only in July and August, but, in con-

TABLE 4. A summary of the major dietary components of underyearling sockeye salmon in 3 zones of the Fraser River estuary, May to September 1977.

	upper Deas Slough								lower Deas Slough										Ladner Reach					
	May		June		July		Sept.		May		June		July		Aug.		Sept.		May		June		July	
Prey item	F[a]	B[b]	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B
Oligochaeta									40*	62	29	16											25	2
Sida crystallina							100*	97																
Bosmina sp.					63	23			20	<1													25	1
Daphnia sp.			66*	25	88*	7	100	<1	20	<1	21	<1	29	<1									25	<1
Moina sp.																					42	4		
Simocephalus serrulatus					44	4			20	<1														
Eurycerus lamellatus					44	1							29	1										
Epischura sp.							100	2	40	1			24	1	25	1							25	13
Cyclops sp.	88*	65	66*	45	81*	47	100	<1	80	<1			59*	40	50*	72								
Macrocyclops albidus					31	1			60	1			18	<1										
Ephemerella sp.									20	<1					20	1			25	5				
Homoptera adults			44	7	10	<1					50	5	24	2	50	2					25	2	50*	9
Diptera pupae	21	1	31	5					40	1	64*	17	35	2	25	3	100	89			83*	23	100*	51
Diptera adults	25	1	41	5					20	<1	21	2	12	2									75	14
Chironomid larvae/pupae	33*	28	34	10	75	15			80*	29	50*	53	71*	44	50*	16			88*	76	42*	53	25	6
Sample size (*n*)	24		32		16		2		8		14		19		4		1		8		12		4	

[a] Frequency of occurrence (%)

[b] Biomass (%)

* Index of relative importance, first and second rank prey items.

TABLE 5. A summary of the prey items and relative biomass (%) consumed by underyearling sockeye salmon which were captured in the Deas Slough and Ladner Reach region of the Fraser River estuary.

Prey	Biomass (%)	Prey	Biomass (%)
ANNELIDA		*Harpacticoida*	<.1
Oligochaeta	3.3	*Halicyclops* sp.	<.1
ARACHNIDA		*Macrocyclops ater*	<.1
Acarina	<.1	Mysidacea	
Araneida	<.1	*Neomysis mercedis*	0.6
CRUSTACEA		Ostracoda	<.1
Cladocera		Amphipoda	
Sida leuchtenbergianum	10.1	*Eogammarus confervicolus*	<.1
Bosmina sp.	6.1	*Hyalella azteca*	<.1
Daphnia sp.	4.6	INSECTA	
Simocephalus serrulatus	1.0	Chironomidae (larvae/pupae)	21.4
Eurycerus lamellatus	0.4	Diptera pupae	2.9
Moina sp.	0.3	Diptera adult	1.3
Sida crystallina	0.2	Homoptera adult	1.2
Chydorus sphaericus	0.2	*Ephemerella* nymph	0.3
Alona affinis	<.1	Heleidae	0.2
Alona rectangula	<.1	Simulidae	0.2
Camptocerus rectirostris	<.1	Plecoptera nymph	0.1
Scapholbereis kingi	<.1	Coleoptera adult	<.1
Copepoda		Trichoptera adult	<.1
Cyclops bicuspidatus thomasii	43.0	Collembola adult	<.1
Cyclops vernalis	0.4	Homoptera nymph	<.1
Epischura nevadensis	0.4	Hymenoptera	<.1
Macrocyclops albidus	0.3	Psocoptera	<.1
Eucyclops agilis	0.2	Fish larvae	0.2
Paracyclops fimbriatus poppei	0.2		
Diaptomus sp.	0.1		

trast to the diet of underyearling sockeye in upper Deas Slough, they were not consumed in June and were relatively minor components of their diet in May.

In the main river channel areas comprising the Ladner Reach zone, insect larvae and pupae were the predominant food. Cladocerans were consumed in relatively small quantities in June and July, and only in July were copepods (*Epischura* sp) consumed.

While recognizing that relatively few underyearling sockeye were examined, it is nevertheless apparent that a greater diversity of major prey items was consumed in the Deas Slough habitat compared to the river channel area of the Ladner Reach zone. Overall, oligochaetes, cladocerans, copepods, and insects were the major food of these fish.

Discussion

JUVENILE SOCKEYE DISTRIBUTION

Based upon a very sparse data set it is inferred that juvenile sockeye salmon (age $\geq 1^+$) only occupied the shallow-water nearshore habitats in the vicinity of Deas Slough for less than 6 wk. Underyearlings, however, were present for a maximum of 21.5 wk.

Sockeye salmon 'smolts' (age $\geq 1^+$) migrate through the Fraser River estuary in a well-defined pulse, centered around the first week in May (Beak Consultants Ltd. 1981). Larger individuals are considered to dominate in the early part of the migration. It is apparent that all are, typically, very transient members of estuarine communities (Healey 1982). In 1977 the first sockeye 'smolt' was recorded on April 27 at the Department of Fisheries and Oceans' Mission sampling station, approximately 75 km upstream from the river mouth. Less than one week later, on May 2, the median of the migration of this age-group of sockeye salmon had been attained. The last sockeye 'smolt' was recorded on June 4, 1977 (M. Bailey, Department of Fisheries and Oceans, pers. comm.). In the same year, the first sockeye 'smolt' (age 1^+) was recorded in the study area on May 9 and the last on June 6.

In 1979 Beak Consultants Ltd. (1981) recorded 97% of their catch of more than 3 000 juvenile sockeye on May 9, during their investigation of fish utilization of the Fraser River estuary. These 'smolts' tended to occupy the centre channel, high velocity waters and, accordingly, were transported seawards more rapidly than sockeye fry which were located in the lower velocity, shallower waters close to the shorelines. Both age 0^+ and 1^+ sockeye were concentrated in the upper surface waters (Beak Consultants Ltd. 1981).

It is apparent that, as commented upon by Barraclough and Phillips (1978), sockeye salmon 'smolts' move rapidly from fresh water to marine waters. Their absence, or scarcity, during detailed investigations of fish populations in the outer regions of the Fraser River estuary supports this view (Goodman 1975; Gordon and Levings 1984; Macdonald 1984; Mesa 1984).

Foerster (1968) mentions 'races' of sockeye salmon which spawn in streams without associated lakes and where the fry migrate directly to sea. In the Kamchatka River in the USSR, 81% of the sockeye were of this type in 1932 (Krokhin and Krogius 1937; cited by Foerster 1968). Recent studies by Wood et al. (1987) also discovered the rearing of sockeye individuals which either migrate directly to sea after emergence or inhabit river channels for at least 1 yr. Sockeye fry which migrated to sea came from populations which spawned in tributaries without access to lake habitats and, in the Iskut River, they migrated seaward at a mean weight of about 1 g and a fork length of 48 mm; not too dissimilar from the underyearling sockeye which occupied the Deas Slough area in 1977. Wood et al. (1987) determined that sockeye fry, which migrated to sea after emergence, contributed 7 to 8% of the total adult production from the Stikine River system.

The presence of underyearling sockeye salmon in Deas Slough in the late spring and early summer, their relatively rapid increase in size and higher condition factors, imply that this area of the Fraser River estuary is an important habitat for successful rearing. The vertically stratified nature of the inner estuary perpetuates a shallow, productive, low salinity (essentially fresh water) environment that is inhabited by many species of fish (e.g. Hoos and Packman 1974; Northcote 1974). Those sockeye salmon with fry which migrate directly to the estuary rather than spend one or more years in fresh water may well have spawning grounds located close to the river mouth (from which migration to the estuary would be relatively rapid). Age 1^+ sockeye migrate seaward from lakes such as Harrison Lake, close to the mouth of the Fraser River. It has been suggested that underyearlings may also migrate from such systems as the Harrison River (Gilbert 1918; Foerster 1968; Northcote 1974) and Widgeon Slough (Pitt River), about 50 km upstream from the mouth (Department of Fisheries and Oceans, unpublished information), thus deriving the benefit of rearing in the essentially fresh to brackish water productive lens of the inner Fraser River estuary.

Underyearling sockeye have been recorded at a number of locations along the Fraser River and in the estuary. For example, in Nicomen Slough, 85 km from the river mouth and in Tilbury Slough (Department of Fisheries and Oceans, unpublished data), in the Duck, Barber, Woodward Island complex of the inner estuary (Dunford 1975; Levy and Northcote 1981, 1982), in Cannery Channel, Steveston, close to the river mouth (Goodman 1975; Anderson et al. 1981; Beak Consultants Ltd. 1981), and on Roberts and Sturgeon Banks in the outer estuary (Goodman 1975; Macdonald 1984). Catches of underyearlings were low at all these locations, but there were similarities in the times at which these underyearling sockeye were recorded. They all occurred in late spring or early summer, reaching peak numbers 1–2 months after the peak of the age $\geq 1^+$ sockeye migration (early May). Numbers of underyearlings in Deas Slough tended to be greater than at other locations where such fish had been recorded, implying that such low flow, backwater areas, in addition to the main river channels, are important rearing areas.

In our study underyearling sockeye salmon were most abundant in upper Deas Slough. They were also the fifth most abundant fish species, out of 21, that were captured in this area. In 1977 their use of this region was greater than that in the lower slough and in the main river channel areas, perhaps indicating the more suitable rearing conditions in the relatively protected upper slough habitat, wherein reduced water flows would be expected to exert less influence on the seaward transport and dispersion of the fry. No similar concentrations of underyearling sockeye have been recorded in the tidally influenced river channel and equivalent estuarine regions of the Fraser River (Dunford 1975; Goodman 1975; Beak Consultants Ltd. 1981; Levy and Northcote 1981, 1982; Macdonald 1984), where more extreme physical conditons exist. If the presence of fry in shallow, nearshore areas, as recorded by Beak Consultants Ltd. (1981), is related to regions with reduced flows, then it would be expected that these fish may reside in low velocity backwater areas such as Deas Slough, assuming the adequacy of other environmental factors, not the least of which is a suitable food supply.

GROWTH AND CONDITION

At their time of arrival in the Deas Slough area, underyearling sockeye salmon differed in length by as much as 30 mm. This could be related to the migration of fish of different size from different stocks, but predominated by the slightly larger fish which are often the first to migrate (Foerster 1968). This latter feature may explain the slightly larger mean length of sockeye (33 mm) on their arrival in Deas Slough in 1977, compared to the mean size (31 mm) recorded two weeks later. After this date, the mean length of the underyearlings increased rapidly until mid-July, and thereafter there was little change.

Underyearlings were similar in length at the same time of year in 1976 and 1977 (about 70 mm, in August). Similarly, Anderson et al. (1981) captured underyearling sockeye with fork lengths of 35–41 mm and 54–67.5 mm in early June and late July 1979, respectively, at the mouth of the Fraser River. In 1981 and 1982, Macdonald (1984) captured underyearlings on Roberts Bank, in the outer estuary. Here the fish were from 43.5 to 71 mm in length between May and August. The fork lengths of age $\geq 1^+$ sockeye are typically about 80 mm at Mission, 75 km above the river mouth, during the downstream migration, and Anderson et al. (1981) determined lengths of this age-group of fish to range from 98 to 103 mm in Cannery Channel, Steveston, in May 1979.

It appears that there is a relatively widespread dispersal of underyearlings in the Fraser River estuary and that a broad size range may be found at most locations. It is also apparent that growth occurs within the system, but whether this is attributable to rearing in the relatively productive slough and other backwater areas of the river and estuary is unknown.

Comparing the size range of underyearling sockeye captured by Dunford (1975) with those taken from Deas Slough, a difference in mean size is apparent. The fish in Deas Slough were larger by about 5 mm in May, and about 20 mm in early July to early August. Because so many factors are likely to influence growth, and also the time of emergence, it may be invalid to compare such data, which were gathered in different years. However, Dunford (1975) collected underyearlings in the Duck–Barber–Woodward Island complex adjacent to Ladner Reach in our study area; hence we may presume that fish in these regions would tend to grow at approximately comparable rates. We found that underyearling sockeye collected from Deas Slough had significantly greater condition factors compared to those collected from Ladner Reach, and also a greater weight for a given size (up to 50 mm). These findings provide additional support for the opinion that Deas Slough is a suitable, if not good, rearing environment for underyearling sockeye. During their period of utilization of the slough, the size of these underyearlings increased rapidly. However, it cannot be assumed that this growth is solely attributable to residents of this area. To our knowledge, no studies have been carried out on the residence of this species in the Fraser River estuary. Accordingly, we must presume that the growth of underyearlings occurred within the Fraser River system and not just in the Deas Slough area, despite the significantly more rapid increase in size and higher condition factors of fish in Deas Slough which imply that the fish were possibly resident there. The elevation in the temperature of the slough, relative to the temperature of the river channel, may be another factor which was conducive to the more rapid growth of the underyearlings (<50 mm length).

The increase in size of fry in the lower Fraser River and estuary would appear to exceed that which Vanstone et al.(1970) recorded in Babine Lake, B.C.; those in our study were about 10 mm longer at comparable time periods. By late summer and early autumn underyearling sockeye in the Fraser River estuary attained a size which was similar to that of some of the 'smolts' (age 1^+) which migrate to sea in the spring. The relatively rapid attainment of this size may be conducive to their subsequent survival in marine waters.

DIET

Information on the diet of underyearling sockeye in the estuary of the Fraser River is confined to a few reports (Dunford 1975; Anderson et al. 1981; Department of Fisheries and Oceans, unpublished data — Tilbury Slough area). Dunford (1975) found that chironomid pupae were the dominant prey, comprising an estimated 65% of total dietary biomass; adult diptera, collembola, and homoptera, and cladocera and copepoda were also consumed. Similarly, Anderson et al.(1981) found that chironomids, cladocerans, and copepods were the most common prey of sockeye captured at the mouth of the Fraser River. In and around Tilbury Slough, further upstream in the estuary, insects were a major prey item, and within the slough cladocerans and copepods were also significant prey (Department of Fisheries and Oceans, unpublished data).

Within upper Deas Slough, copepods, cladocerans, and insects predominated in the diet of underyearling sockeye. Oligochaetes, copepods and insects were heavily utilized in lower Deas Slough and, similar to the findings of Dunford (1975) and Anderson et al.(1981), insects were also the primary prey at the river chanel locations.

The consumption of copepods and cladocerans by underyearling sockeye in the slough habitats of the Fraser River estuary approximately parallels their diet in lake environments (for example, Chapman and Quistorff 1937; Foerster 1968; Eggers 1978; Fedorenko et al. 1979).

At the river channel sampling sites in our study area, the diet of underyearling sockeye was similar to that determined for both underyerling and age $\geq 1^+$ sockeye in similar locations in that insects were the dominant prey, with crustaceans as other major items (Chapman and Quistorff 1937; Northcote 1974; Dunford 1975; Northcote et al. 1979). Northcote (1974) found that 99% of sockeye juveniles captured in the lower Fraser River had food (mainly insects) in their stomachs and concluded that considerable feeding occurs during their down-river passage, thereby emphasizing the importance of the river benthic invertebrate communities as an energy source during their migration. The results of our studies would endorse this statement.

Anderson et al. (1981), however, upon examining relatively few specimens, found that the majority of migrating age 1⁺ fish close to the Fraser River mouth were not feeding, and those that were had consumed mysids and harpacticoids. From our own investigation, it is deduced that not only do the main river channels provide rearing habitat and food for juvenile sockeye, but that slough habitats, such as Tilbury Slough and to a greater extent Deas Slough, contribute substantially in this regard.

In that cladocerans and copepods are typical dietary constituents of underyearling sockeye in lake environments, their substantial consumption in Deas Slough implies an abundance of such prey; notwithstanding the probable movement of fish in and out of this area. This, and possibly other features, may well be conducive to the aggregation of underyearling sockeye in slough habitats for significant periods of time. Based upon the rapid increase in size of underyearlings in Deas Slough (no comparable information exists for river channel areas upstream of the estuary during downstream migration), and the extensive, 21.5 wk utilization period, we suspect that underyearling sockeye reside, at least temporarily, in the Deas Slough area. As mentioned previously, we cannot, however, eliminate the possibility of different and increasing size classes of underyearlings entering (and leaving) the study area during the utilization period.

WATER CHARACTERISTICS AND SOCKEYE PRESENCE

Marked seasonal changes in levels of certain aquatic variables occur in Deas Slough and Ladner Reach. During the study, fluctuations in measured variables were influenced primarily by Fraser River flow and salt water intrusion. During the winter, low freshwater-flow period, salinities increased in Deas Slough, less so in the upper regions than in lower Deas Slough and Ladner Reach. Water clarity improved in winter, while temperature, dissolved oxygen and oxidation-reduction potential values tended to decrease at this time (Department of Fisheries and Oceans, unpublished information). In the deeper waters of Deas Slough, in dredged pockets adjacent to two marinas, one in the upper, the other in the lower portion of the slough, dissolved oxygen depression was common, and values less than 10% of air saturation were recorded. Contrasting with this situation were the high levels of dissolved oxygen that were maintained throughout the year in shallow waters (0.5 m depth); the minimum values experienced by underyearling sockeye were 77% of air saturation.

When juvenile sockeye salmon were present in shallow surface waters of Deas Slough and adjacent habitats, the physical conditions of their environment were relatively stable and at levels generally not expected to be stressful to them. However, it is also apparent that aquatic conditions in the upper slough area during the period of utilization by sockeye were more variable than conditions within the river channel area. Elevated temperatures and reduced levels of dissolved oxygen (often marked at depth) could restrict full use of the water column. According to Davis' (1975) dissolved oxygen criteria, dissolved oxygen levels in the deeper water of Deas Slough would be, at times, lethal to salmonids. In surface waters, minimum values of about 77% of air saturation were close to those which are known to be stressful (Davis 1975), but average values were at levels considered to confer a high degree of safety.

The absence of underyearling sockeye in the study area when the maximum (23°C) temperature was recorded may reflect their avoidance of potentially lethal or harmful conditions (Brett 1952). When lower temperatures subsequently prevailed, sockeye were again captured, but in very low numbers.

Salinity values in surface waters were relatively uniform and low while juvenile sockeye were in the Deas Slough area, and therefore not expected to have influenced distributions in these waters. There was, however, an inference from collections of fish made on Roberts and Sturgeon Banks that larger underyearlings were to be found in higher salinity waters, up to 9.5‰ (Department of Fisheries and Oceans, unpublished data). Inadequate data prevent no more than an inference from being drawn.

In comparison to observations made in the inner estuary of the Somass River, B.C., juvenile sockeye salmon were found to inhabit waters with similar dissolved oxygen levels (77–116% of air saturation), temperatures (9–18°C), salinities 0.1–8.1‰, pH values 7.1–7.8, and oxidation-reduction potential values from + 166 to + 305 (Department of Fisheries and Oceans, unpublised data). Only salinity values are substantially different from those recorded in the Deas Slough study area.

In summary, we consider that the variations in aquatic characteristics we examined probably exerted little influence on the horizontal distribution of sockeye salmon in the Deas Slough area. Most probably the relatively high utilization of the area was associated with the comparatively protected, permanently wetted, low water velocity conditions within Deas Slough and food resources similar to those consumed by underyearling sockeye while in fresh water. The relatively long utilization period, high "apparent growth" rate, and condition factors of fish taken from the slough strongly infer that underyearling sockeye derive some benefit from their temporary residence in this area during late spring and summer, thus contrasting with age ≥ 1⁺ sockeye which are very transient members of the estuarine communities. In addition, these findings emphasize the need to continue to research the biology of fish in the Fraser River system, and to identify and maintain their aquatic habitat. The ecology of most of the diverse fishery resources within this extensive watershed is not well known, and the provision of this information will greatly assist in fisheries management decisions.

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Scale Patterns and Biology of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in the Kamchatka River

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Abstract

BUGAEV, V. F. 1987. Scale patterns and biology of juvenile sockeye salmon (*Oncorhynchus nerka*) in the Kamchatka River, p. 36–43. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Seven distinct stocks or groups of sub-stocks of sockeye salmon, *Oncorhynchus nerka*, can be differentiated using differences in scale structure and the prevalence of infection by tapeworms (*Diphyllobothrium* sp.). These characteristics are attributed to stock-specific differences in juvenile life history and freshwater rearing habitat. Smolts from one group are predominantly age 0., and from other groups, either age 1. or age 2.. Most groups also comprise both early (spring) and late (summer) seasonal races. The Soviet fishery exploits these groups at different rates owing to differences in run timing.

Résumé

BUGAEV, V. F. 1987. Scale patterns and biology of juvenile sockeye salmon (*Oncorhynchus nerka*) in the Kamchatka River, p. 36–43. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Sept stocks ou groupes de sous-stocks de saumon nerka (*Oncorhynchus nerka*) peuvent être identifiés au moyen des différences scalimétriques et de la fréquence de l'infection par des cestodes (*Diphyllobothrium* sp.). Ces caractéristiques sont attribuées à des différences propres à chaque stock pour ce qui est du cycle vital des juvéniles et de l'aire de croissance en eau douce. Les smolts d'un groupe particulier sont pour la plus grande partie d'âge 0. tandis que ceux d'autres groupes, soit d'âges 1. ou 2.. La plupart des groupes comptent aussi des remontes saisonnières hâtive (printemps) ou tardive (automne). La pêche soviétique exploite ces groupes à différents taux à cause des variations du moment de la remontée.

Introduction

According to Dobzhansky (1950, 1955, 1970), species occur as assemblages of "Mendelian" populations which can be distinguished at several levels of geographic range, i.e., subspecies, races, or local populations. Whereas the term "population" has an evolutionary significance, the term "stock" may be applied to any population, or a group of individuals for which a single management, or fishing strategy is appropriate (Kuznetsov and Mina 1982). Indeed, the sockeye salmon (*Oncorhynchus nerka*) tends to occur in discrete, local stocks throughout its geographic range (Foerster 1968; Smirnov 1975; Konovalov 1980).

The Kamchatka River basin supports some of the largest Asian stocks of sockeye salmon, and in some years the largest Soviet sockeye fishery (Ostroumov 1964, 1972). Early investigations of the biology of the Kamchatka sockeye provided some evidence for the existence of "second order stocks" or "sub-stocks" within sockeye populations of the river basin (Krogius 1970) but these studies were inconclusive. Data collected in 1975–80 provide a more complete picture of the biology of the most important of these sub-stocks (Bugaev 1978, 1981a, b, 1982, 1983a, b, c, 1984a, b; Bugaev and Karpenko 1983). The main conclusions from these investigations are presented here.

Methods

A total of 4753 sockeye fry, and 5912 spawners were sampled from 29 sub-stocks (Fig. 1) from 23 tributaries to examine variation in the life history of Kamchatka sockeye and to develop criteria for differentiating them. Both scale structures and prevalence of infection by tapeworm parasites of the genus *Diphyllobothrium* were recorded. The prevalence of *Diphyllobothrium* plerocercoids was determined for 4105 spawners and 1950 fry. Scales were removed from the area below the dorsal fin just above the lateral line as described by Pravdin (1966). Scale images were examined at 100× magnification using a microprojector.

Bands of closely-spaced sclerites are referred to as "zones of adjacent sclerites" (ZAS); these may be formed annually ("annuli") or at other times. The presence or absence, or number of sclerites in these ZAS often differs among sub-stocks (Bugaev 1978). For example, in the Kamchatka River, a "river-type" ZAS can be distinguished from a typical "lake-type" ZAS since the former comprises fewer sclerites

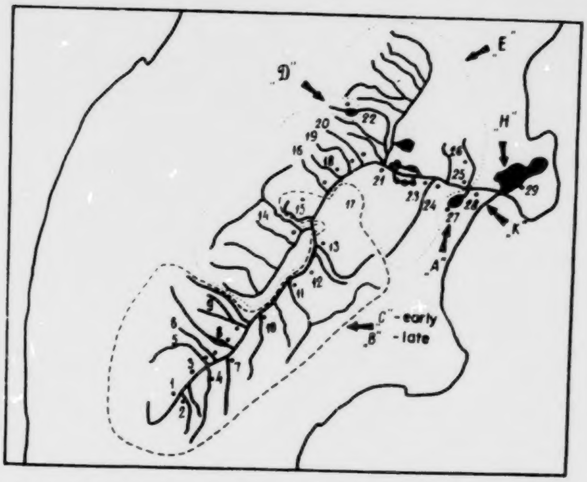

FIG. 1. The Kamchatka River basin (diagrammatic) showing sampling sites for sockeye spawners: 1 — Puschino village, 2 — Kashkan River, 3 — Sharoma village, 4 — Kavycha River, 5 — Andrianovka River, 6 — Zhupanka River, 7 — Vakhvina River (Valagina), 8 — Kirganik River, 9 — Kimitina River, 10 — Kitilgina River, 11 — Shchapina River, 12 — Nikolka River springs, 13 — Tolbachik River, 14 — Bystraya-Kozyrevka River, 15 — Shekhlun River, 16 — Kreruk River, 17 — Ushkovskoe Lake springs, 18 — Kryuki River, 19 — Polovichnaya River, 20 — Belaya River, 21 — Yelovka River, 22 — Lake Dvukhyurtochnoe, 23 — Bolshaya Khapitsa River, 24 — Malaya Khapitsa River, 25 — Raduga River, 26 — Nizovtsevo Lake (Raduga River drainage), 27 — Azabachye Lake, 28 — Kursin Lake, 29 — Soldatskaya River (Nerpichye Lake drainage).

Ed. Note: Group symbols "*B*", "*C*", and "*H*" are transliterated in text as *V*, *S*, and *N*, respectively.

(0–2 compared with 3–8). Lake-type ZAS are found only in sockeye which feed and grow in Dvukhyurtochnoe, Azabachye, Nerpichye, and Kursin lakes before emigrating to sea as smolts (Bugaev 1978). Following Bugaev (1978, 1983b, 1984a and b), indistinct ZAS were recorded as having "zero sclerites".

Results

The following stocks and groups of sub-stocks were distinguished on the basis of the scale patterns of fry and spawners, and the presence or absence of infection by *Diphyllobothrium* sp.:

1. *Sockeye sub-stocks of the upper and middle reaches of the Kamchatka River, whose fry migrate downstream to sea as age 0. fingrlings ("S" group).*

Some sub-stocks spawning in the upper and middle Kamchatka River can be distinguished from other stocks in the watershed on the basis of the spacing between sclerites in the central zone of their scales. In fact, any sockeye in the Kamchatka River with sclerites in this zone spaced more than 3.2 mm apart (at 100× magnification) is likely to belong to this group (the "*S*" group) of early (spring) sub-stocks (Fig. 2 and 3). The only exception to this rule, are late (summer) run sockeye that spawn in Ushkovskoe Lake where early run sockeye are rare (Ostrowmov 1975).

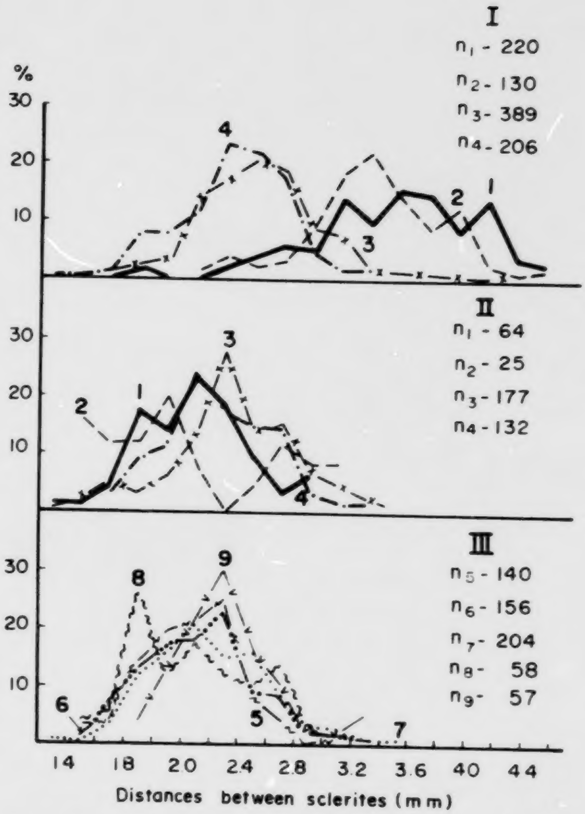

FIG. 2. Mean distance between sclerites on the scales of sockeye spawners and fry in the Kamchatka River basin (magnification ×100). Fish with less than 5 sclerites in the first growth zone of their scales were excluded.

I — Distance between sclerites in the first zone of growth (including the first ZAS) of the 1976 early spawning Kamchatka River sockeye from: 1 — Upper reaches of the river and its tributaries where sockeye are not infected by *Diphyllobothrium* sp.; 2 — Basins of the middle reaches of the river where sockeye are not infected by *Diphyllobothrium* sp. (some lake sockeye from the Ushkovskoe Lake springs are included); 3 — Tributaries of the middle and lower reaches of the river where sockeye are not infected by *Diphyllobothrium* sp.; 4 — All lakes combined (except Nerpichye Lake).

II — Distances between sclerites on the scales of juvenile sockeye from rearing areas of the Kamchatka River in the region of Pushchino–Klyuchi: 1 — At Pushchino; 2 — Milkovo to the Shchapina River; 3 — old side channels from Dolinovka to Tolbachik River; 4 — Ushkovskoye lake springs.

III — Distance between sclerites for rearing areas in the region of Klyuchi River to the mouth of the Kamchatka River: 5 — Flood plain lakes; 6 — Azabachye Lake and its outlet stream; 7 — the main bed channel lakes and side channels of Raduga River; 8 — Kursin Lake; 9 — Kamchatka River estuary.

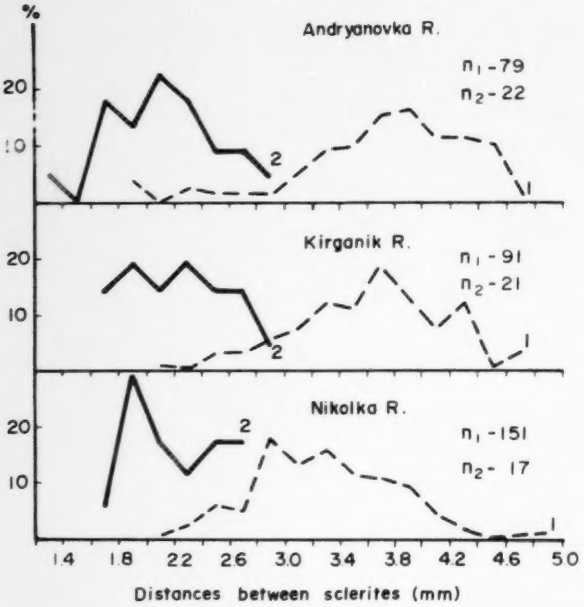

FIG. 3. Mean distance between sclerites in the first zone of growth (including first ZAS) on the scales of early (1) compared with late (2) spawning sockeye. Samples over a number of years are pooled (magnification ×100). Fish with fewer than 5 sclerites in the first zone of growth were excluded.

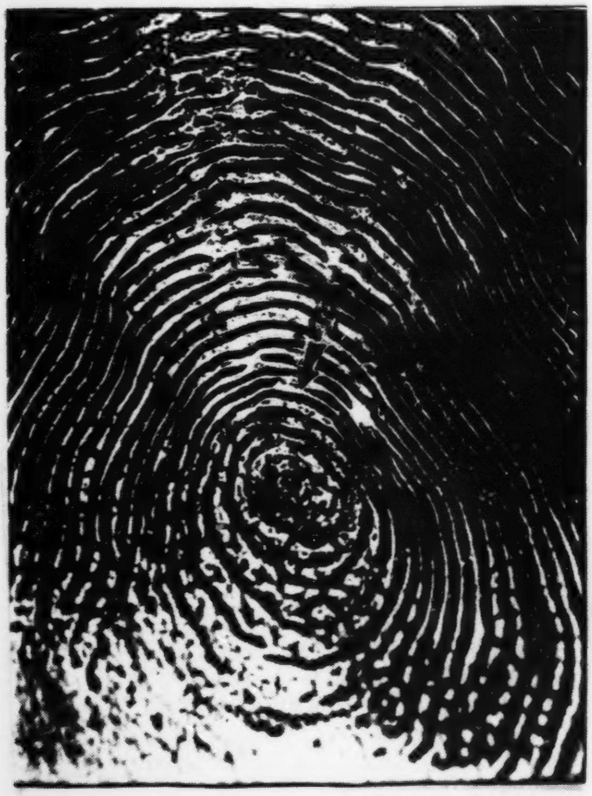

FIG. 4. Central part of the scale of a typical "*S*" group sockeye. Arrow shows river type ZAS. Source: Andryanovka River, 1977: freshwater age 0+.

The widely spaced sclerites in the central zone of the scale suggest that "*S*" group sockeye migrate to sea as fingerlings before the scales are well formed. Other investigations have shown that growth in salt or brackish water results in more widely spaced sclerites than does growth in fresh water (Bugaev and Karpenko 1983; Bugaev 1984a).

Most "*S*" group scales have an indistinct or badly expressed central area characterized by one (often weak) river-type ZAS (Fig. 4 and 5). The ZAS illustrated in Fig. 4 developed in salt water and does not reflect the seasonal rhythm of growth (i.e., it is not an annulus). The reason for these false annuli is not yet known. "*S*" group spawners are not infected with *Diphyllobothrium* sp. and are mainly age 0.3.

2. *Sockeye sub-stocks of the upper and middle reaches of the Kamchatka River whose fry rear in the river near the parental spawning grounds before migrating downstream as age 1. smolts ("V" group).*

Although some fry originating in spawning grounds in the upper and middle reaches of the Kamchatka River migrate to sea as fingerlings (the "*S*" group), the majority spend

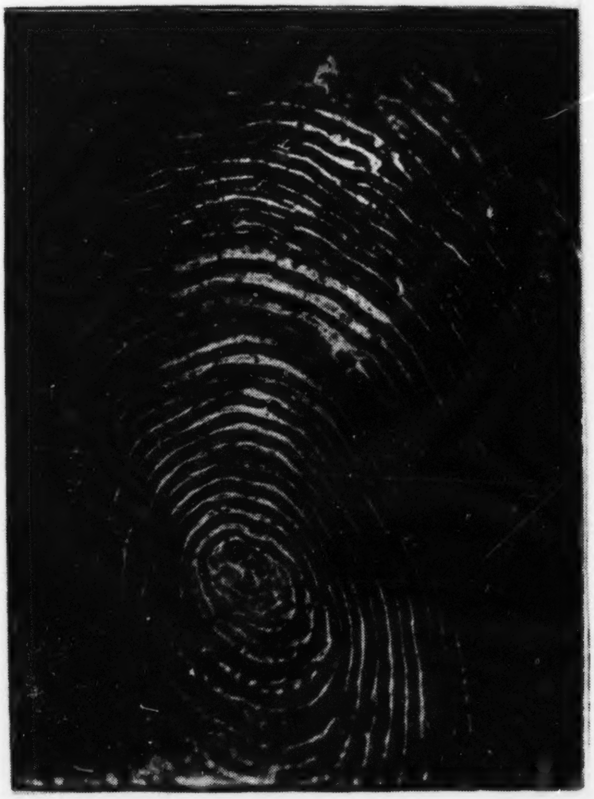

FIG. 5. Central part of a scale from an "S" group sockeye without a ZAS. This specimen was collected from Ushkovskoe Lake springs in 1977 and had spent 1 year in fresh water.

the winter in fresh water in the vicinity of the spawning grounds (the "*V*" group). The following year during seaward migration, a characteristic scale pattern is formed (Fig. 6, 7): after the first 6–10 sclerites, an additional number (commonly 6–8) occur which are more widely spaced. The first zone corresponds to the growth which takes place in the river near the spawning grounds, the second, to growth during the seaward migration. The latter corresponds to the "compensational growth" of Mina and Klevezal (1976). One reason for this compensational growth may be that fingerlings migrate from the upstream spawning area when water temperatures in the lower river and lakes near the outlet are warmer, and that the fry enter these areas and forage for a short time (Mina and Klevezal 1976). In some years, zones of compensational growth may be absent on scales of late sockeye of the upper Kamchatka River basin (Fig. 8). The "*V*" group spawners are not infected with *Diphyllobothrium* sp. and are mainly age 1.3 fish.

3. *A sockeye stock spawning in Azabachye Lake whose fry rear in the lake before emigrating to sea as age 2. smolt ("A" group).*

Scales from sockeye spawning in Azabachye lake ("*A*" group sockeye) typically have two lake-type ZAS (Fig. 9) which implies that the majority of "*A*" group juveniles spend 2 years in fresh water. On average, scales from 10% of "*A*" group spawners have an additional river-type ZAS. This anomalous group may comprise "*E*" group sockeye (see below) that have strayed during their return migration. The extent of reproductive isolation between "*A*" and "*E*" group sockeye has not yet been investigated. Almost all "*A*" group spawners are age 2.3 and are infected with *Diphyllobothrium* plerocercoids.

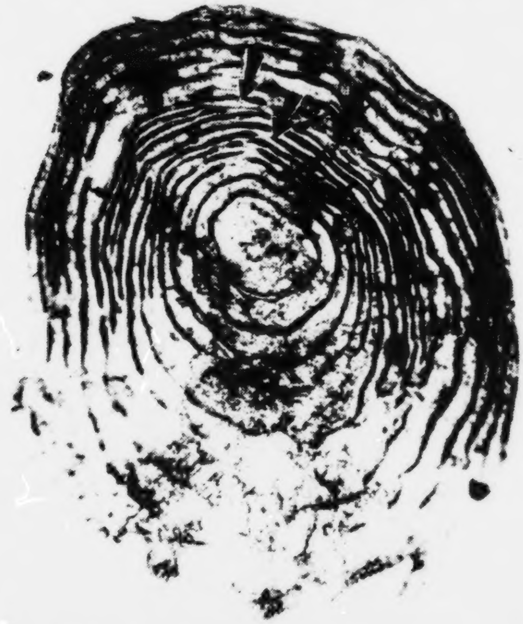

FIG. 6. A typical scale of juvenile, group "*V*" sockeye. Arrows indicate two ZAS (first ZAS is an annulus). This specimen was collected from the middle reaches of the Kamchatka River, June 16, 1977, when it was 10.6 cm. in length and age 1+. The second ZAS is thought to be associated with the beginning of migration from the spawning grounds and the start of compensatory growth.

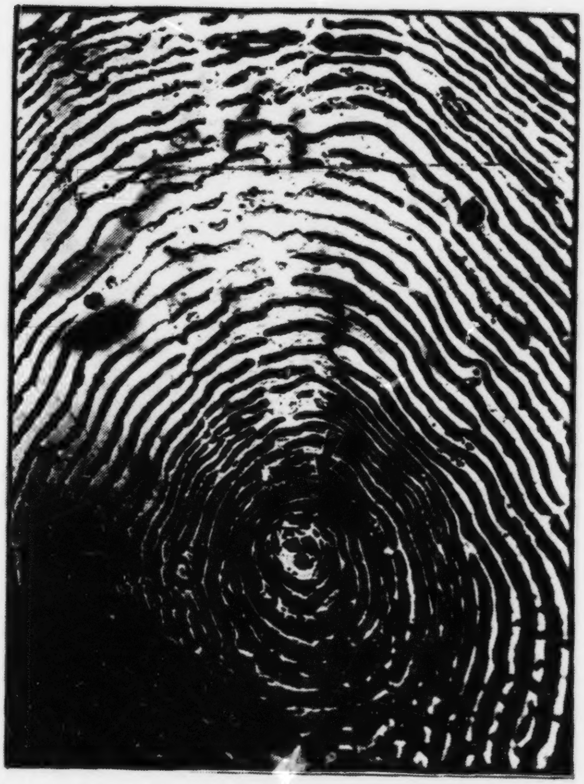

FIG. 7. Central part of a typical scale from group "*V*" sockeye spawners. Arrow indicates ZAS. Source: Kirganik River, 1978; freshwater age 1+.

4. *Sockeye sub-stocks of the middle and lower reaches of the Kamchatka River whose fry rear in Azabachye Lake before emigrating to sea as age 1. smolt ("E" group).*

Bugaev (1981b, 1982) concluded that sockeye fry from the middle and lower reaches of the Kamchatka River migrate downstream as fingerlings to Azabachye Lake where they spend the winter before migrating to sea as age 1. smolts. This conclusion is supported by the existence of density-dependent growth of juveniles within Azabachye Lake. It is well known that fish growth can be influenced by population density (Nikolsky 1974) and that variations in growth rate are recorded in scale patterns (Burgner 1964; Ward and Larkin 1964; Mathisen and Kerns 1964; Burgner et al. 1967; Mathisen 1969; Parr and Burgner 1971; Goodlad et al. 1974).

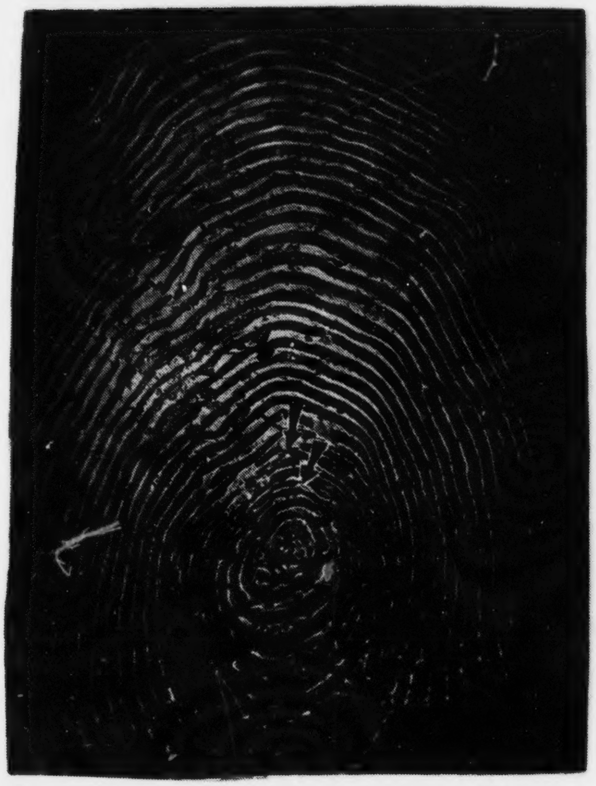

FIG. 8. Central part of a typical scale from group "*V*" sockeye spawners. Arrows indicate the two ZAS; the first ZAS is the annulus. Source: Nikolka River springs, 1978; freshwater age 1+.

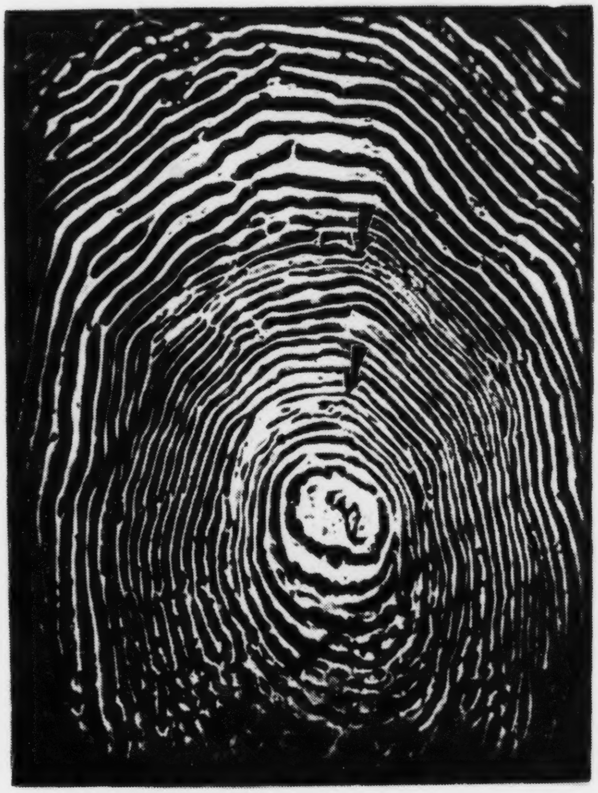

FIG. 9. Central part of a typical scale from stock "*A*" sockeye spawners. Arrows indicate the two ZAS which are both annuli. Source: Azabachye Lake, 1975; freshwater age 2+.

The growth rate of juvenile sockeye in Azabachye Lake (inferred from the scales of adult sockeye spawning in Azabachye Lake) is inversely correlated with the abundance of "*E*" group spawners and with the abundance of "*A*" group spawners. This suggests that juveniles from these groups forage together in Azabachye Lake.

Scales from "*E*" group spawners have an additional ZAS which is not an annulus. This ZAS forms after migration from the spawning tributaries to Azabachye Lake in July–November (Bugaev 1981b) owing to the abrupt change in habitat and feeding conditions. A second ZAS, the annulus, forms later in the year. Thus, at the time of seaward migration, "*E*" group sockeye have both a typical annulus (or lake-type ZAS) and a less distinct river-type ZAS (Fig. 10). Using this criterion to differentiate the "A" and "E" groups, it appears that 60–70% of juveniles in Azabachye Lake are "*E*" group fish (Bugaev 1981b). The majority of "*E*" group sockeye spawn at age 1.3 and are infected with *Diphyllobothrium* plerocercoids.

5. *A sockeye stock whose fry rear in Nerpichye Lake before emigrating to sea as age 1. smolts ("N" group).*

Nerpichye Lake is the largest brackish water lake in northeastern Asia. Bugaev (1984b) concluded that fry rearing in Nerpichye Lake migrated there from spawnings areas in the upper tributaries of the Kamchatka River. The scale features of "*N*" group sockeye are similar to those of "*E*" group sockeye in that both comprise two ZAS: a weak, river-type ZAS followed by a lake-type ZAS (Fig. 11). The distance between sclerites in the first zone of growth is usually 3.0–3.2 mm (at 100× magnification). In contrast to "*E*" group juveniles, most "*N*" group juveniles migrate to Nerpichye Lake before their scales have formed. This implies that the weak, river-type ZAS forms in the lake, but for unknown reasons. The second lake-type ZAS is a true annulus. The majority of "*N*" group sockeye spawn at age 1.3 and are not infected by *Diphyllobothrium* plerocercoids.

6. *A sockeye stock whose fry rear in Dvukhyurtochnoe Lake before emigrating to sea as age 2. smolts ("D" group).*

The sockeye stock associated with Dvukhyurtochnoe Lake differs from other sockeye stocks in the Kamchatka River with respect to the number of sclerites (>10) (Fig. 12) and width of scales formed during growth in fresh water (Fig. 13). The scales of "*D*" group sockeye have two (lake-type) ZAS which are annuli; there are no additional river-type ZAS. The "*D*" group spawning population has tended to remain stable at a low abundance owing to the lack of spawning habitat in the vicinity of Dvukhyurtochnoe Lake. Consequently, scale patterns also tend to be consistent from year to year. The spawners are typically age 2.3 and are infected with *Diphyllobothrium* plerocercoids.

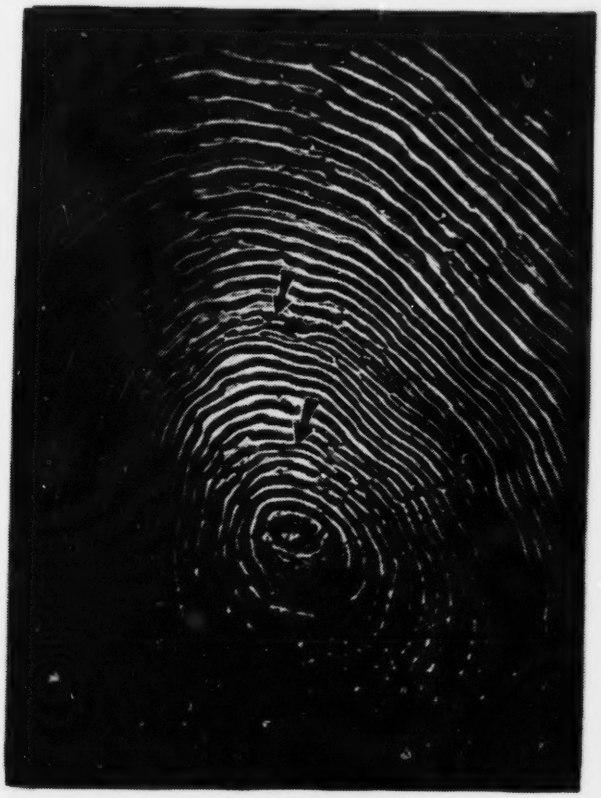

FIG. 10. Central part of a typical scale from group "*E*" sockeye spawners. Arrows indicate the two ZAS; the second ZAS is the annulus. Source: Bolshaya Khapitsa River, 1978: freshwater age 1+.

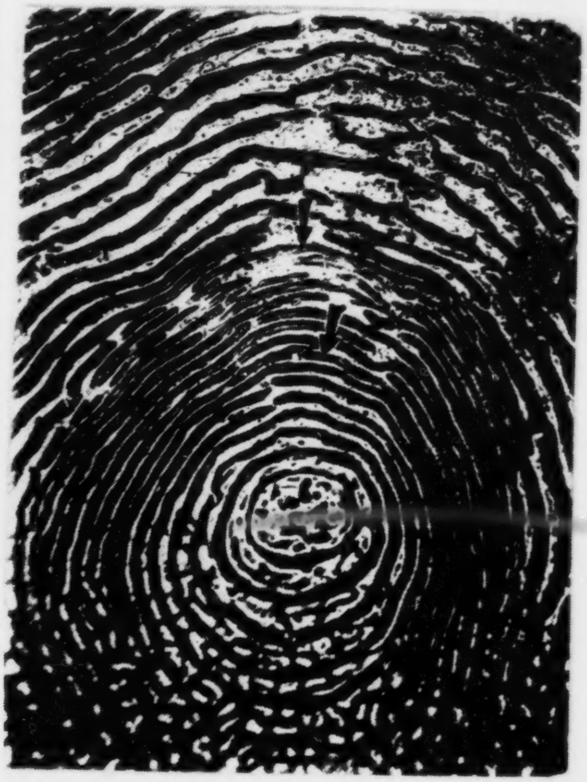

FIG. 11. Central part of a typical scale from group "*N*" sockeye spawners. Arrows indicate the two ZAS: The second ZAS is the annulus. Source: Nerpichye Lake, 1977: freshwater age 1+.

7. *A sockeye stock whose fry rear in Kursin Lake before emigrating to sea as age 1. smolts ("K" group).*

The Kursin Lake system comprises two lakes — Big Kursin Lake and Little Kursin Lake. An early sockeye run spawns in Big Kursin Lake. Scale patterns differ between sockeye from these two lakes although typically, both have two ZAS in the central part of their scales. Scales of early run Kursin sockeye are similar in type and pattern to those of the "*E*" grouping and cannot be differentiated from them on the basis of criteria now available. The first ZAS on these scales is thought to be formed as a result of juveniles migrating from the first to the second lake whereas the second ZAS is an annual ring. Late run Kursin sockeye have two ZAS in the freshwater growth zone, with an average of 10 sclerites in the first, 6 sclerites in the second, and 2–3 more sclerites on the scale margin. The first ZAS is usually of the lake type and the second, of the river type. The small number of sclerites and indistinct pattern of the second ZAS are characteristic (Mina 1973; Bugaev 1978), but the reasons for their formation is not yet known. Most "*K*" group sockeye spawn at age 1.3 and are not infected with *Diphyllobothrium* plerocercoids. Migration of sockeye fry from Kamchatka River to the Kursin lakes has not been observed.

Discussion

These investigations demonstrate that Kamchatka River sockeye salmon have a complex population structure consisting of both discrete stocks and groupings of sub-stocks. Differences in scale patterns associated with growth in fresh water and the presence or absence of *Diphyllobothrium* infection in spawning sockeye reflect the different juvenile life histories of separate stocks and sub-stocks within the watershed. All of the discrete stocks ("*A*", "*N*", "*D*", and "*K*" groups) and one group of sub-stocks (the "*E*" group) comprise both early (spring) and late (summer) seasonal races. The other groups of sub-stocks comprise only a single seasonal race each — the "*S*" group spawns early and the "*V*" group spawns late — but both spawn in the same regions of the Kamchatka River watershed (Fig. 1).

I consider these seasonal races to be "second order stocks" or "subisolates" as defined by Konovalov (1980) because they are self-perpetuating and utilize different spawning grounds. Each seasonal race is distinct genetically or

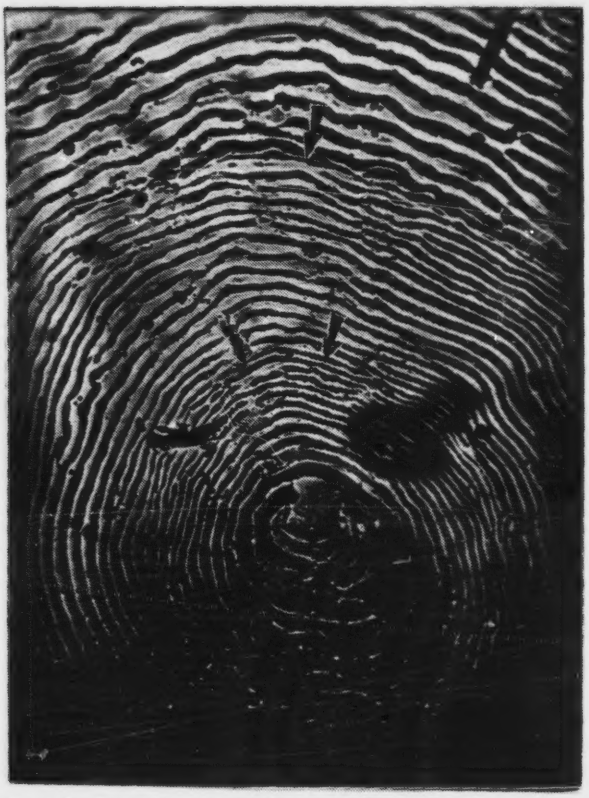

FIG. 12. Central part of a typical scale from group "*D*" sockeye spawners Arrows indicate the two ZAS both of which are annuli. Source: Dvukhyurtochnoe Lake, 1976; freshwater age 2+.

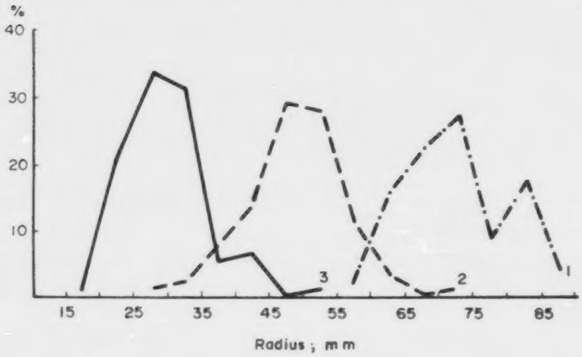

FIG. 13. Frequency distributions of the width of the second ZAS (magnification ×100) on scales of sockeye spawners in Dvukhyurtochnoe and Azabachye lakes. 1 — Dvukhyurtochnoe Lake, 1975 (n = 44); 2 — Azabachye Lake, 1977 (n = 78); 3 — Azabachye Lake, 1973 (n = 73). Sockeye fry were much more abundant in Azabachye Lake in 1973 than in 1977.

ecologically and tends to have characteristic scale patterns and age composition. The concept of "subisolates" was developed by Konovalov (1980) following his investigations of sockeye life history in the Azabachye Lake basin. Others (Yarzhombeck and Klyashtorin 1980; Mina and Griftsenko 1981) have argued that the concept must be defined more precisely and that further study is required to verify Konovalov's (1980) conclusions. This skepticism is warranted in light of findings presented here, that juvenile sockeye from sub-stocks in the lower Kamchatka River rear together with those from the Azabachye Lake stock.

The stocks and groups defined here differ greatly in abundance. In the years of observation (1957–1983), the average stock composition (with ranges given in parentheses) was as follows: "*S*" group, 25.9% (4.3–57.7%); "*A*", 16.2% (3.7–43.1%); "*D*", 3.4% (0.5–14.6%); and "*K*", 0.1% (<0.1–0.6%). These stocks and sub-stock groupings are exploited at different levels by Soviet fisheries because of differences in their time of spawning migration.

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Review of the Ecological Significance of Diel Vertical Migrations by Juvenile Sockeye Salmon *(Oncorhynchus nerka)*

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Abstract

LEVY, D. A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (*Oncorhynchus nerka*), p. 44–52. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Juvenile sockeye within their nursery lakes commonly undertake diel vertical migrations such that they occur in deeper water by day than by night. Light and temperature appear to serve as orienting stimuli during these migrations, controlling the day and night vertical distributions respectively. Three existing hypotheses which may explain the significance of diel vertical migration are reviewed. The foraging strategy hypothesis is rejected because zooplankton prey organisms concentrate in shallower water than juvenile sockeye during daylight hours and often have negligible vertical movements. The bioenergetic hypothesis whereby energetic efficiency serves as the selective pressure behind migration is plausible but does not account for the usual timing of migrations. Likewise the predator avoidance hypothesis, which postulates predation by visual-feeding piscivores as a selective force, is also plausible. Under certain sets of limnological conditions the latter two hypotheses make conflicting predictions concerning diel vertical migration by juvenile sockeye. Thus it should be possible to test if one is in error, or whether a multifactor hypothesis is required to explain this behavioral phenomenon.

Résumé

LEVY, D. A. 1987. Review of the ecological significance of diel vertical migrations by juvenile sockeye salmon (*Oncorhynchus nerka*), p. 44–52. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les saumons nerkas juvéniles effectuent des migrations verticales nycthémérales dans leurs lacs de croissance de sorte qu'on les retrouve à plus grande profondeur le jour que la nuit. La lumière et la température semblent être les stimuli orientant ces migrations et régissant, respectivement, les distributions verticales de jour et de nuit. L'auteur fait l'examen de trois hypothèses actuelles pouvant expliquer l'importance de la migration verticale nycthémérale. L'hypothèse reposant sur une stratégie de recherche de la nourriture est rejetée car les organismes proies du zooplancton se concentrent dans des eaux moins profondes que celles où se trouvent les saumons nerkas juvéniles au cours des heures d'éclairement et que ces organismes ont souvent des déplacements verticaux négligeables. L'hypothèse bioénergétique reposant sur l'efficacité énergétique comme pression sélective s'avère plausible, mais ne permet pas d'expliquer le moment où s'effectue normalement les migrations. De façon analogue, l'hypothèse d'évitement des prédateurs, qui suppose la prédation par des organismes piscivores décelant leurs proies visuellement en tant qu'élément sélectif, s'avère aussi plausible. Dans certaines séries de conditions limnologiques, l'application de ces deux dernières hypothèses donne des prévisions opposées de la migration verticale nycthémérale des saumons nerkas juvéniles. Il devrait donc être possible d'effectuer un test pour savoir si l'une des hypothèses est fausse ou s'il faut faire appel à une hypothèse à facteurs multiples pour expliquer ce phénomène comportemental.

Introduction

Diel vertical migration is widespread in fishes; it occurs in pelagic and demersal marine species (Woodhead 1966), in freshwater fishes (Northcote et al. 1964; Dembinski 1971) and in some forms such as sockeye in both freshwater and marine environments (Brett 1983). Sockeye salmon juveniles commonly undertake diel vertical migrations covering tens of metres while they are resident in the pelagic zone of their nursery lakes. Because juvenile sockeye are visual-feeding planktivores (Foerster 1968), their occurrence in the relatively shallow euphotic zone where zooplankton concentrate would seem to be advantageous to prey acquisition. Furthermore, descent below this zone necessarily involves energy expenditures (Alexander 1971, 1972) and foregone feeding opportunities. For diel vertical migration behavior to have evolved, ecological benefits must be realized by juvenile sockeye migrants that compensate for these costs.

There are three existing hypotheses which account for the ecological significance of diel vertical migrations by juvenile sockeye: a foraging strategy hypothesis, a bioenergetic hypothesis (Brett 1971), and a predator avoidance hypothesis

(Eggers 1978). In this article existing information on juvenile sockeye vertical migrations is reviewed, the relative importance of the above three mechanisms is evaluated, and a new, multifactor hypothesis is proposed.

Patterns of Diel Vertical Migration by Juvenile Sockeye and Kokanee

Diel vertical migration is defined herein as a synchronized movement by aquatic organisms in the vertical plane which has a periodicity of 24 h. The migration involves a regular alternation between spatially separated day and night depth strata. Diel vertical migrations are common in planktonic animals (see reviews by McLaren 1963; Hutchinson 1967; Longhurst 1976; and Dingle 1980), and are also well known among fish on the basis of observed day–night differences in catches by commercial fishermen (Woodhead 1966). For juvenile sockeye in nursery lakes, diel vertical movements can be inferred from tow-netting studies (e.g., Johnson 1956) which indicated maximum surface catches during dusk periods. With the advent of scientific echo sounders, precise documentation of juvenile sockeye diel vertical migration patterns became feasible.

Diel vertical migrations by juvenile sockeye were first described in Babine Lake (Narver 1970). During summer periods, juvenile sockeye in this lake ascend from their daytime depth between 20–40 m into surface waters at dusk (Fig. 1). Echo traces and tow-net catches made during the night indicate nocturnal descents to the vicinity of the thermocline, followed by a brief re-ascent close to the surface at dawn. Thereafter, in the early morning hours, there is a gradual descent to the daytime depth level.

Sockeye underyearlings undertake diel vertical migrations both in relatively clear transparent lakes as well as in glacially turbid ones. The vertical amplitude of migration and details of timing vary in different populations. Juvenile sockeye at Babine Lake ascend vertically towards the surface at dawn and dusk and cover a vertical amplitude of about 20 m (Fig. 2). In Lake Washington there is a single dusk ascent and surface (0–5 m) waters are avoided (Woodey 1972). Juvenile sockeye in Great Central Lake can occur below 100 m in daylight hours and swim through vertical distances as great as 70 m (Barraclough and Robinson 1972). In Lake Tustumena, a heavily glacially turbid lake situated on the Kenai Peninsula (Alaska), diel vertical migration is reversed with juvenile sockeye distributed close to the surface by day and occupying deeper water at night (Thorne 1983). This unusual pattern probably results from severe light extinction which permits visual feeding only close to the surface during daylight hours. In Owikeno Lake, a glacial lake with turbidity conditions less extreme than Lake Tustumena, trawl catches indicate that juvenile sockeye follow the usual pattern of diel vertical movements, ascending close to the surface at dusk, and descending at dawn (Chernoff 1971).

During daylight periods, juvenile sockeye in Babine Lake, Lake Washington, and Great Central Lake, are on occasion distributed vertically in a bimodal pattern and concentrated in two discrete depth strata (Narver 1970; Woodey 1972; Barraclough and Robinson 1972). At Babine Lake, the two depth strata were centered at about 20 and 35 m, and each was about 6 m in thickness (Narver 1970). This daytime depth segregation may be the result of feeding activity by part of the juvenile sockeye population. Babine Lake fish in the uppermost (20 m) depth strata were actively feeding on

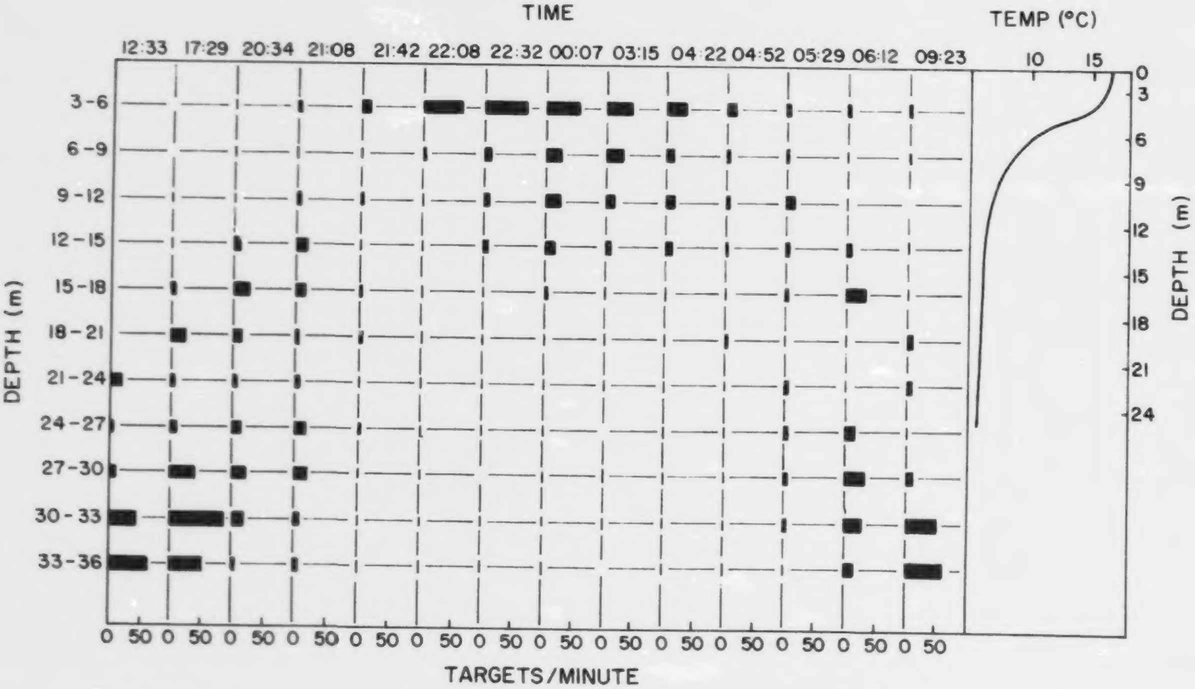

FIG. 1. Depth frequency of juvenile sockeye salmon at Babine Lake on Aug. 5–6, 1967 as estimated by counting echotargets obtained with a 175 kHz Honeywell echosounder. Vertical temperature profile shown on the right. Reproduced from Narver (1970).

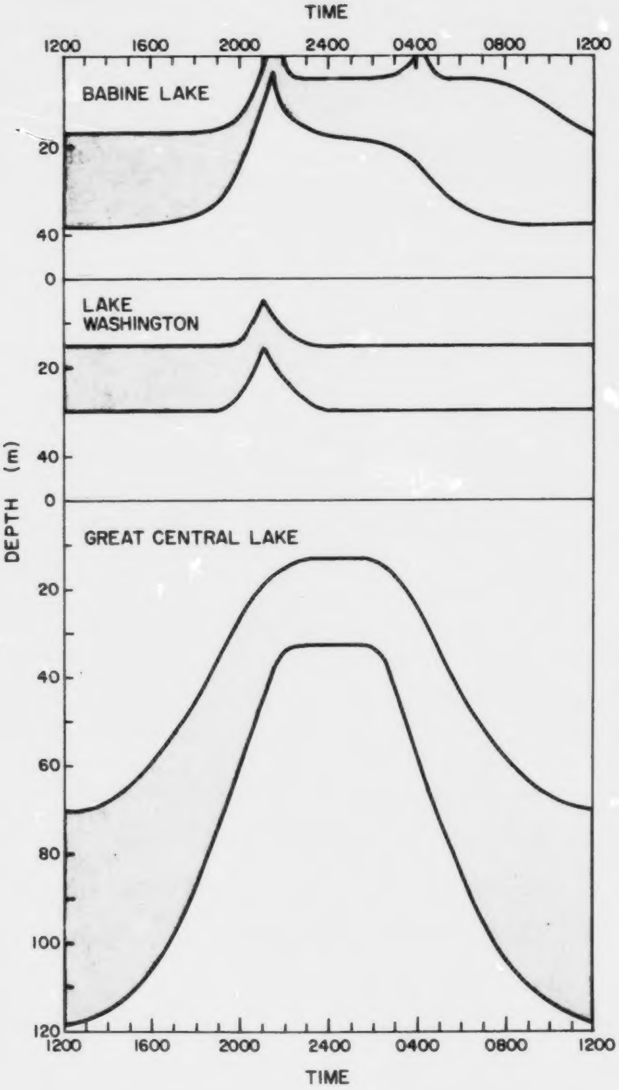

FIG. 2. Diel variation in mid-summer juvenile sockeye depth distribution in Babine Lake, Lake Washington and Great Central Lake. Data from Narver (1970), Woodey (1972), and Barraclough and Robinson (1972), respectively. Shaded area indicates depth range occupied by juvenile sockeye.

the calanoid copepod *Heterocope septentrionalis*, in contrast with non-feeding fish in the lower (35 m) depth strata (Narver 1970). A similar depth stratification of feeding and non-feeding fish into upper and lower depth strata respectively occurred during daylight periods within Lake Washington (Woodey 1972).

Schooling is conspicuous among juvenile sockeye in fresh water. Eggers (1978) has shown a close correlation between the 0.17 lux isolume and the location of schooled fish targets on echograms taken from Lake Washington. At dusk, as light intensities diminished, schooled fish targets disappeared from echograms indicating school dispersal during hours of darkness. The schools evidently re-formed with increasing light intensity after dawn. Schooling did not occur in winter months but resumed during the growth period prior to smolt migration (Eggers 1978).

Juvenile sockeye are planktivorous and forage primarily in the higher portions of the water column at dawn and dusk in both Babine Lake (Narver 1970) and Great Central Lake (Barraclough and Robinson 1972). In Lake Washington, they forage during a single dusk feeding episode (Doble and Eggers 1978). Crustacean zooplankton, including most of the commonly occuring cladocerans and copepods, serve as the predominant food of juvenile sockeye in the pelagic zone of their nursery lakes (Foerster 1968; Narver 1970; Barraclough and Robinson 1972; Woodey 1972; McDonald 1973; Doble and Eggers 1978).

Diel vertical migrations by juvenile sockeye begin soon after pelagic zone residency is established. Fry emerged from Babine Lake tributaries in May and were observed in the littoral zone of the lake for several weeks in late May-early June of 1966 (McDonald 1969). Between June 25–July 27, 1966, juvenile sockeye were captured in pelagic purse seine sets during the night but not during the day, providing evidence of diel vertical movements (McDonald 1969). During the fall (October, 1967) juvenile sockeye in Babine Lake undertook diel vertical migrations that extended between a daytime depth range of 18–40 m and a night-time depth range of 9–27 m (Narver 1970). Juvenile sockeye migrated vertically in Lake Washington during November of 1970 (Woodey 1972). There is no published information on diel vertical movements by juvenile sockeye during winter months, although Brett (1983) suggests that such movements do not occur. During seaward migration, yearling sockeye smolts evidently change their diel vertical migration behavior. At Babine Lake, schools of migrating smolts have been observed in surface waters by day (Johnson and Groot 1963) and were seined in shallow littoral areas of Morrison Arm during daylight hours (Westwater Research Centre, The Univ. of B.C., Vancouver, B.C., Canada, unpublished data).

Juvenile sockeye usually pass through different temperature zones when migrating vertically. In Babine Lake, they migrate from the cold hypolimnion through the thermocline and into the epilimnion (Fig. 3) encountering temperature differences as much as 12°C (Narver 1970; McDonald 1973). The night-time period is usually spent in the vicinity of the thermocline (Fig. 1 and 3). In sockeye lakes close to the southern range of the species (e.g., Lake Washington) warm summer epilimnetic temperatures (>20°C) can limit the ascent by juveniles (Woodey 1972). During summer months, juvenile sockeye vertical migrants in Lake Washington experience temperature differences of 4–5°C (Woodey 1972).

Juvenile sockeye may at times migrate vertically under isothermal conditions. At Babine Lake during October, 1967 when most of the water column was isothermal at 8°C, trawl samples indicated that juvenile sockeye occupied a day-time depth range between 15–30 m (Fig. 3). At neighboring locations, McDonald (1973) captured sockeye juveniles at night in surface waters by a purse seine. These net catches suggest that juvenile sockeye in Babine Lake continue to migrate vertically under isothermal temperature conditions. In Lake Washington during autumn, temperature differences of usually less than 1°C were encountered by juvenile sockeye while undertaking their diel vertical migrations (Woodey 1972).

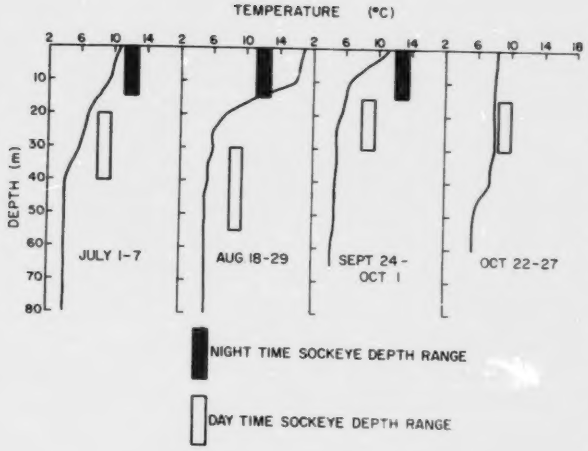

FIG. 3. Juvenile sockeye day and night depth ranges in Babine Lake shown in relation to temperature profiles. Data from McDonald (1973).

Kokanee, the lake-locked form of sockeye salmon, undertake reversed diel vertical migrations in several lakes at least, and occur in shallower waters by day than by night at certain times of the year. Kokanee in Nicola Lake were shown to have a reversed diel vertical migration during 8 out of 10 intensive 24 h netting series conducted during the summer and fall months (Northcote et al. 1964; Northcote 1967). Peamouth chub in Nicola Lake undertook vertical migrations diametrically opposite to those of kokanee and alternated between deep water during the day and surface waters at night. Temperature conditions in Nicola Lake were most frequently isothermal through the period that kokanee and peamouth chub migrated vertically (Northcote et al. 1964). In Babine Lake, McDonald (1969) captured kokanee in shallow (0–16 m) purse seine sets by day indicating that in this lake, kokanee are surface oriented during daylight hours. In Pend Oreille Lake, Idaho, summer echo sounding studies (Riemen and Bowler 1980) indicated that kokanee were distributed between 0–20 m during daylight hours and between 18–27 m during the night.

Sensory Mechanisms

The diel vertical movements of aquatic organisms are often crepuscular suggesting that light serves as a primary sensory stimulus. Deep scattering layers in the ocean, comprised partially of myctophid fishes (Backus et al. 1968; Barham 1966) undertake diel vertical migrations that are associated with changes in light intensity (e.g., Boden and Kampa 1967). The role of light in vertical migrations of fish has been reviewed by Woodhead (1966) and Blaxter (1974) who observed that some vertical migrants such as herring follow the vertical movement of particular isolumes. At high latitudes, both in the Arctic and Antarctic Oceans, diel vertical migration of fish is absent (Blaxter 1974). Deep scattering layers respond to solar eclipse by ascending and descending as light intensities decrease and increase (Backus et al. 1965) and can be displaced with artificial lights. On one occasion near the Canary Islands, a deep scattering layer was experimentally displaced downwards from 60 to 300 m (Blaxter and Currie 1967).

The crepuscular timing of diel vertical migration suggests that juvenile sockeye respond to a light stimulus. Water clarity characteristics may affect the amplitude of juvenile sockeye vertical migration. The relatively deep daytime distribution in Great Central Lake (70–120 m) and the large amplitude of vertical movement there (Fig. 2) is probably related to the deep light penetration into this lake. Narver (1970) reports a September Secchi depth of 14 m for Great Central Lake compared with 4 m for Babine Lake. At Lake Tustumena during June of 1981 when there was virtually no dark period due to its high latitude, juvenile sockeye did not migrate vertically (Thorne 1983).

Fish are highly temperature-sensitive and possess sophisticated thermoregulatory behaviors (Rozin and Mayer 1961; Neill et al. 1972). The sensory system responsive to temperature is the general cutaneous segmental innervation (Sullivan 1954; Murray 1971). During conditioned response experiments (reviewed by Murray 1971) a majority of fish tested were sensitive to temperature changes of between 0.05–0.1°C. Smith (1985) has suggested that predictable thermal gradients might be used as orienting stimuli in fish migrations and there are numerous examples (reviewed by Reynolds 1977) of temperature serving as a proximate stimulus affecting movements and hence distribution of fish populations.

The nocturnal distribution of juvenile sockeye in lakes suggests that the fish might be responding to a temperature stimulus. At night juvenile sockeye commonly stay in the vicinity of the thermocline (Narver 1970; McDonald 1973). During the period of thermal stratification of Lake Washington, fish were distributed in a narrow range of temperatures (Fig. 4) between 7.6–11.0°C, about 4°C lower than the preferred 12–15°C in laboratory-induced vertical temperature gradients (Brett 1952).

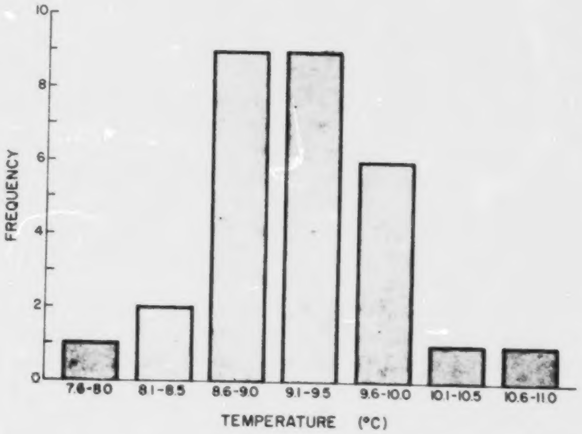

FIG. 4. Frequency distribution of temperatures at which maximum nocturnal trawl catches of juvenile sockeye were made during the period of thermal stratification of Lake Washington during 1970. Data from Woodey (1972).

In summary, both light and temperature cues may serve as orienting stimuli for juvenile sockeye during their diel vertical movements. Day-time depth distrubution and the timing of vertical movements suggest that fish follow a particular range in light intensities. Night-time depth distribution suggests thermoselection by the fish.

Ecological Significance of Diel Vertical Migration

1) *Foraging strategy hypothesis:* Juvenile sockeye are largely planktivorous during their period of lake residence (Foerster 1968; Doble and Eggers 1978) so necessarily must overlap with zooplankton populations in time and space. The foraging strategy hypothesis is based on the idea that diel vertical movements result from the fish pursuing and following concentrations of vertically migrating prey organisms so as to maximize capture rates and minimize search time. At least some planktivores including alewives in Lake Michigan (Janssen and Brandt 1980) and freshwater sardines in Lake Kariba (Begg 1976) track the diel vertical movements of their zooplankton prey. There are additional potential foraging benefits of vertical migration to planktivores. A vertically ascending planktivore has the advantage of a lighted background to provide visual contrast with its zooplankton prey (Zaret and Suffern 1976), an important factor in fish vision. As well, a vertical migrant might be able to "census" its prey organisms (Woodhead 1965) especially if horizontal currents operated in different depth strata. Diel vertical migration would reduce the probability of re-encountering plankton patches that had been locally depleted due to previous foraging activity.

For juvenile sockeye, the foraging strategy hypothesis seems unlikely since zooplankton in at least several sockeye lakes concentrate in shallower water than do juvenile sockeye. In Great Central Lake juvenile sockeye descend far below zooplankton populations (Fig. 5). Zooplankton diel vertical movements are negligible in Great Central Lake (Le Brasseur and Kennedy 1972) and Lake Washington (Eggers1978). *Heterocope septentrionalis* and *Bosmina coregoni* are the only two zooplankters that migrate vertically in Babine Lake (Narver 1970), the former migrating to a day-time depth of 15–30 m and the latter undertaking a reversed diel vertical migration. It is thus evident that for sockeye to maximize their foraging success on zooplankton, day and night residence in the portion of the water column where zooplankton concentrate would be advantageous over diel vertical migration. Such discrepancies between the distribution and movement patterns of fish and zooplankton appear to invalidate the foraging strategy hypothesis as an explanation for diel vertical movements by juvenile sockeye.

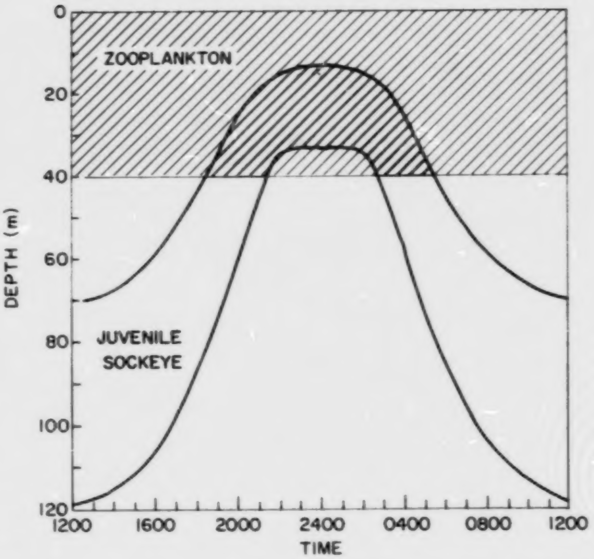

FIG. 5. Diel variation in juvenile sockeye and zooplankton depth distribution in Great Central Lake. Data from Barraclough and Robinson (1972) and LeBrasseur and Kennedy (1972), respectively.

2) *Bioenergetic hypothesis:* There exists good empirical evidence that juveniles of some sockeye populations are food-limited during their lake residency: when such sockeye lakes are artificially fertilized smolt sizes increase and marine survival rates are enhanced (Hyatt and Stockner 1985). The density-dependent growth rates that have been observed at Babine Lake (Johnson 1961) and Owikeno Lake (Ruggles 1966) further indicate that juvenile sockeye often grow at less than maximum rates. This freshwater growth limitation and the observation that vertically migrating juvenile sockeye pass through markedly different temperature zones led Brett (1971) to propose the bioenergetic hypothesis as an explanation for juvenile sockeye diel vertical migration. The idea is an extension of McLaren's (1963) hypothesis that vertically migrating zooplankton in thermally stratified waters would achieve an energetic advantage (compared to non-migrants) if they reduced their day-time metabolic costs in cold hypolimnetic water. Calculations for juvenile sockeye in Babine Lake (Fig. 6) indicated the possibility of metabolic cost reductions and Brett (1971) concluded that "sockeye have evolved a pattern of thermoregulation peculiarly adapted to maximizing growth, through the selective pressure of bioenergetic efficiency".

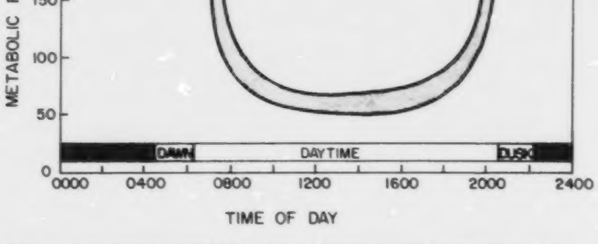

FIG. 6. Estimated metabolic rate of juvenile sockeye salmon during a midsummer day at Babine Lake. Reproduced from Brett (1971).

Laboratory evidence suggests that diel vertical migration by juvenile sockeye has energetic consequences. Biette and Geen (1980) reared sockeye under controlled constant and cyclic temperatures (fluctuating on a diel time scale) and found that when food rations were low highest growth rates occurred in fish exposed to cyclic temperatures. Similar experimental results were obtained with juvenile rainbow trout where diel temperature fluctuations were shown to be beneficial to growth (Hokanson et al. 1977). While diel temperature fluctuations evidently promote faster fish growth, it may be erroneous to accept this as evidence confirming the bioenergetic hypothesis. Vertically migrating fish, especially those with swimbladders, incur significant energy costs in order to compensate for the accompanying hydrostatic changes (Alexander 1971, 1972). These costs were not considered by Biette and Geen (1980) and would effectively diminish a growth advantage due to diel temperature fluctuations. Calculations by Alexander (1972) suggest that the energetic cost to a vertical migrant with a swimbladder, of hydrodynamic compensation at its daytime depth, is on the order of 25 cm^3 oxygen • kg^{-1} • h^{-1}. The reduction in resting metabolic rate of a 5 g teleost at 5°C, compared to 15°C has been calculated by Fry (1957, cited in Alexander 1972) as 40 cm^3 oxygen • kg^{-1} • h^{-1}. Thus, it appears that at least half of the energetic advantage of metabolism at a lower temperature would be offset by the additional energetic cost of maintaining neutral buoyancy. Although these considerations do not rule out the bioenergetic hypothesis, they imply that the metabolic benefits of vertical migration by juvenile sockeye would be less than previously suggested.

3) *Predator avoidance hypothesis:* Among certain freshwater zooplankton, diel vertical migration is evidently caused by intensive predation pressure from visually dependent planktivores (Zaret and Suffern 1976; Stich and Lampert 1981). Eggers (1978) hypothesized that juvenile sockeye in Lake Washington keep to regions of the water column where light intensity is low and limit their foraging time so as to minimize the possibility of being seen by squawfish, a visual-feeding piscivore.

The fact that juvenile sockeye school by day suggests an influence of predators since schooling can function as a predator avoidance mechanism (Cushing and Harden Jones 1968; Neill and Cullen 1974). Juvenile sockeye experience considerable mortality (>90% in some lakes) during their period of lake residence (Foerster 1938; Brett and McConnell 1951), primarily due to predation by piscivores (Ricker 1941). Predation by Dolly Varden char and cutthroat trout on juvenile sockeye occurs under the ice in mid-winter at Lakelse Lake (Foerster 1968). In Cultus Lake juvenile sockeye are exposed to intense predation pressure from squawfish, Dolly Varden, cutthroat trout, and juvenile coho (Ricker 1941) and a 3-fold increase in lake survival rates followed a predator control program (Foerster and Ricker 1941).

The predator avoidance hypothesis cannot presently be rejected nor confirmed. Some sockeye lakes are reputed to have very few predatory fish and estimated lake survival rates are relatively high. For example Port John Lake appears to have few piscivores (Robertson 1954) and survival rates from fry to age II smolts range between 19–84% (Foerster 1968). However, the diel vertical migration behavior of juvenile sockeye in such lakes has not been described.

Discussion

Based upon the information presented in this review neither the bioenergetic hypothesis nor the predator avoidance hypothesis can be rejected outright. However, there appear to be some promising opportunities for testing these hypotheses and evaluating whether both are necessary and sufficient causes of diel vertical migration by juvenile sockeye.

During daylight hours, under conditions of a shallow thermocline juvenile sockeye locate deep in the hypolimnion (Fig. 1). Under such conditions, a large portion of the diel vertical migration occurs in the cold hypolimnion (e.g., 12–36 m depth in Fig. 1) under uniform temperature conditions. Contrary to the statement by Brett (1983) that diel vertical movements cease during the fall when the entire water column becomes isothermal, observations by McDonald (1973) and Woodey (1972) indicate that such movements may in fact continue. Confirmed migration by juvenile sockeye under isothermal conditions would cast doubt on the bioenergetic hypothesis since all temperature-dependent physiological functions surely would then occur at the same rate.

For a visual-feeding planktivore, day-time occurrence in the illuminated surface waters where prey concentrate would seem to be advantageous over a day-time distribution at depth where light levels are low and prey are often sparse or absent. A reversed vertical migration by juvenile sockeye, whereby the fish occupied surface waters by day and deep water at night, would result in similar energetic costs to those pertaining in the normal diel vertical migration pattern. However, the increased zooplankton foraging opportunities would presumably result in higher growth rates, particularly among sockeye populations which are food-limited in fresh water.

Brett (1971) dismissed the predator avoidance hypothesis because of observations by Narver (1970) of low predator densities in the pelagic zone of Babine Lake. However, Eggers (1978) pointed out that the absence of piscivores in the pelagic zone may be the result of effective antipredator behavior by juvenile sockeye and the existence of alternative more profitable littoral prey organisms. At Cultus Lake, squawfish shifted from the pelagic zone into the littoral zone between May and September and altered their diet from juvenile sockeye to cyprinids, sticklebacks, terrestrial insects, and plankton (Ricker 1941). These observations suggest that piscivores in sockeye lakes are responsive to alternative energy sources and, therefore, their importance as sockeye predators may be seasonal.

Under some limnological conditions, the bioenergetic and predator avoidance hypotheses lead to conflicting predictions concerning vertical migration behavior. For instance, in glacially turbid lakes having a deep thermocline, e.g., Owikeno Lake (Fig. 7), the bioenergetic hypothesis predicts migration below the thermocline. In contrast the predator avoidance hypothesis requires solely that the fish descend to regions of low light intensity which, in a glacially turbid lake, would be relatively high up in the water column. Juvenile sockeye in Owikeno Lake have been sampled with a trawl net and evidently migrate vertically (Chernoff 1971), but the data do not permit reconstruction of the diel vertical migration pattern.

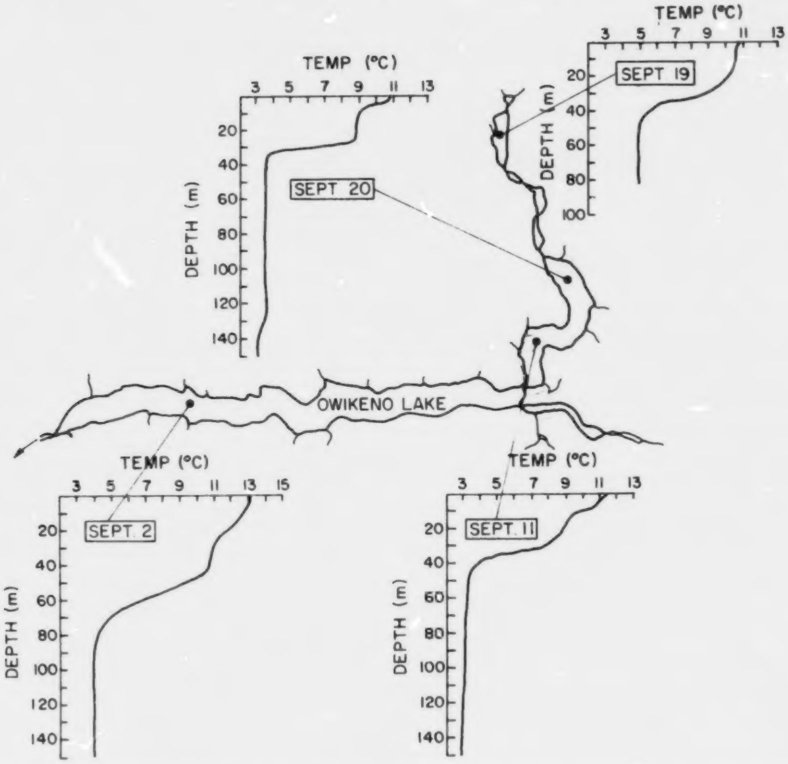

FIG. 7. Temperature profiles from Owikeno Lake obtained during September of 1952. Data from Foskett (1958).

Sockeye lakes having uniform temperature conditions also predict conflicting behavior since it is not possible to achieve bioenergetic benefits by migrating under isothermal conditions. However, piscivores undoubtedly forage under such temperature conditions and the predator avoidance hypothesis predicts active diel vertical migration by juvenile sockeye independent of temperature conditions.

Numerous recent studies confirm that fish foraging behavior often represents a trade-off between energetic returns and predation risk (e.g., Dill 1983; Dill and Fraser 1984; Gilliam 1982; Milinski 1986; Werner and Gilliam 1984). Furthermore, Hilborn and Stearns (1982) argue that many ecological and evolutionary phenomena are complex processes that require multifactor hypotheses. Both the predator avoidance and the bioenergetic hypotheses may contribute to diel vertical migration behavior in juvenile sockeye. A multifactor hypothesis can be stated (following Gilliam 1982): diel vertical migration is a foraging behavior that serves to minimize the ratio of mortality risk to energetic return in juvenile sockeye. In most animals, hunger (or the absence thereof) can provide an index of energetic profitability within a habitat. Monitoring mortality risk is possible when prey species routinely encounter their predators, e.g., bluegills encountering bass in the littoral zone of a lake (Gilliam 1982). However, planktivores like juvenile sockeye would rarely encounter their predators in a lake's pelagic zone. Gilliam (1982) has suggested that habitat selection in such animals would depend upon an evolved affinity for habitat structure.

A major difficulty encountered when testing theories of risk sensitive foraging is that energetic returns and predation risk are measured in disparate currencies (Dill 1983). In future, one promising area of investigation will involve comparisons of diel vertical migration behavior under diverse sets of limnological conditions. Such comparisons may well provide useful insight into different mechanisms influencing diel migratory behavior of juvenile sockeye in their lake nursery environments.

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Are the Migrations of Juvenile and Adult Fraser River Sockeye Salmon (*Oncorhynchus nerka*) in Near-Shore Waters Related?

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Abstract

GROOT, C., AND K. COOKE. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? p. 53–60. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Sockeye salmon (*Oncorhynchus nerka*) returning to the Fraser River from their ocean feeding grounds migrate either via a northern or southern route around Vancouver Island. The proportion taking the northern route has varied annually from 2 to 80% over the last 33 years. Sockeye smolts leaving the Fraser River on their way to the ocean can also follow either route around Vancouver Island. The purpose of this study was to test the hypothesis that adult sockeye salmon return to the Strait of Georgia and the Fraser River by retracing the same route taken as juveniles during seaward migration. The migratory routes of sockeye salmon smolts through the Strait of Georgia on their way to the Pacific Ocean were determined by sampling their distribution by seining and two-boat trawling during spring and early summer of 1982–1984. Combining these results with additional information from previous studies, indicated that most smolts left inland waters by moving north. Two patterns were evident; (i) a migration in which smolts leaving the Fraser River immediately turned north and continued to travel along the mainland coast, (ii) a movement of smolts across the Strait of Georgia towards the Gulf Islands and then continuing north along the east side of these islands and diagonally northward through the Strait to join the smolts migrating along the mainland shore. This suggests that Fraser River sockeye smolts have a north to northwestern directional tendency. The movement from the rivermouth across the Strait of Georgia towards the Gulf Island is assumed to result from a combination of strong river outflow and tidal currents. Comparison of the migratory patterns of the juveniles and the adults indicate that they are not related and that the hypothesis that the outward migration of juveniles determines the inward migration of adults, cannot be substantiated. It is suggested that the smolts perform a one-directional compass orientation (north to northwest) and the adults show goal orientation by being able to home in to the Fraser River from their ocean feeding grounds by either following a northern or a southern route around Vancouver Island.

Résumé

GROOT, C., AND K. COOKE. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? p. 53–60. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci 96.

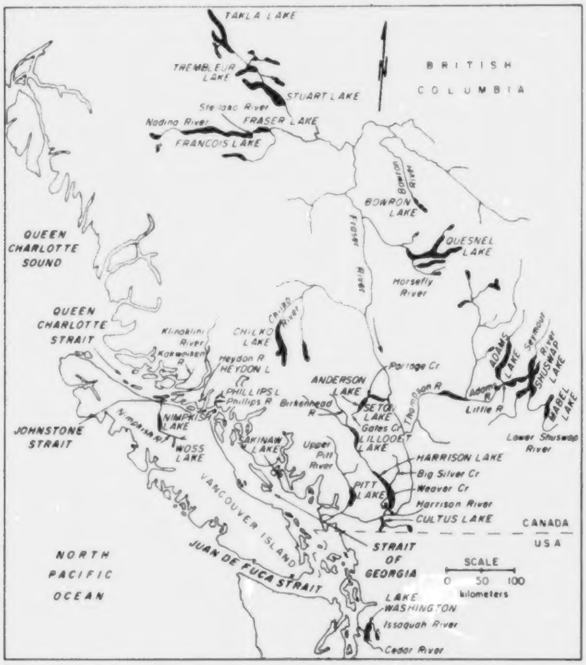
Le saumon nerka (*Oncorhynchus nerka*) qui revient des aires d'alimentation océaniques vers le fleuve Fraser contourne l'île de Vancouver par le nord ou le sud. Au cours des 33 dernières années, le pourcentage qui a utilisé la route septentrionale a varié annuellement de 2 à 80 %. Les smolts de saumon nerka qui quittent le fleuve Fraser en direction de l'océan peuvent aussi contourner l'île de Vancouver par ces deux routes. Les auteurs veulent vérifier l'hypothèse que les saumons nerkas adultes reviennent au détroit de Géorgie et au fleuve Fraser en utilisant le même itinéraire qu'ils ont suivi à l'état de juvénile au cours de la migration vers la mer. Dans le détroit de Géorgie, les routes migratoires des smolts en route vers l'océan Pacifique ont été déterminées par relevé de leur distribution à l'aide du sennage et d'un chalutage à deux bateaux menés au cours du printemps et au début de l'été de 1982 à 1984. Ces résultats combinés à des données supplémentaires obtenues au cours d'études antérieures ont révélé que la plupart des smolts ont quitté les eaux intérieures en se déplaçant vers le nord. Deux régimes migratoires étaient évidents : i) une migration au cours de laquelle les smolts qui quittaient le fleuve Fraser se sont immédiatement dirigés vers le nord et ont suivi le littoral continental et ii) la traversée du détroit de Géorgie vers les îles Gulf suivie d'un déplacement vers le nord le long de la côte est de ces îles pour ensuite se diriger diagonalement vers le nord par le détroit et rejoindre les smolts qui migraient le long du littoral continental. Ceci porte à croire que les smolts du fleuve Fraser ont tendance à se diriger vers le nord ou le nord-ouest. On croit que la traversée du détroit de Géorgie à partir de l'embouchure du fleuve vers les îles Gulf est le résultat d'un débit fluviatile élevé et des courants de marée. Une comparaison des régimes migratoires des juvéniles et des adultes révèle qu'ils ne sont pas en relation et que l'hypothèse selon laquelle la dévalaison des juvéniles détermine la montaison des adultes ne peut être étayée.

On pense que les smolts exécutent une orientation unidirectionnelle magnétique (du nord au nord-ouest) et que les adultes montrent une orientation dirigée étant donné qu'ils sont capables de gagner le fleuve Fraser à partir de leur aire d'alimentation océanique en contournant l'île de Vancouver par le nord ou le sud.

Introduction

Sockeye salmon (*Oncorhynchus nerka*) pass through a number of greatly differing habitats during their life cycle. After emergence from the gravel, the fry usually migrate to nursery lakes where they spend a year or more before migrating downstream to the ocean as smolts. In the ocean they move north from the overwintering grounds in spring and early summer and south again when temperatures drop in late summer and autumn (French et al. 1976). Then, when the adults start to mature after one (for jacks), two, or more years in the ocean, they return to the home river and lake tributary to spawn and die.

When adult sockeye salmon return to the Fraser River from their ocean feeding grounds they take one of two routes around Vancouver Island: the northern route via Queen Charlotte and Johnstone straits, or the southern route via Juan de Fuca Strait (Fig. 1). The proportions of the total run using each route has varied substantially during the last 33 years (IPSFC 1954–86). From 1953 to 1977, the majority homed via the southern route (average 84%, range 65–98%). Since 1978, more sockeye have migrated via the northern route (average 48%, range 22–80%).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BOWRON LAKE
Fraser River
QUESNEL LAKE
Horsefly River
QUEEN CHARLOTTE SOUND
QUEEN CHARLOTTE STRAIT
Klinaklini River
Kakweiken R
CHILKO LAKE
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Heydon R
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ANDERSON LAKE
Portage Cr
Birkenhead R
SETON LAKE
Gates Cr
Thompson R
Adams R
ADAMS LAKE
Seymour River
SHUSWAP LAKE
MABEL LAKE
Little R
Lower Shuswap River
JOHNSTONE STRAIT
Nimpkish R
NIMPKISH LAKE
WOSS LAKE
SAKINAW LAKE
Upper Pitt River
LILLOOET LAKE
HARRISON LAKE
Big Silver Cr
Weaver Cr
PITT LAKE
Harrison River
CULTUS LAKE
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USA
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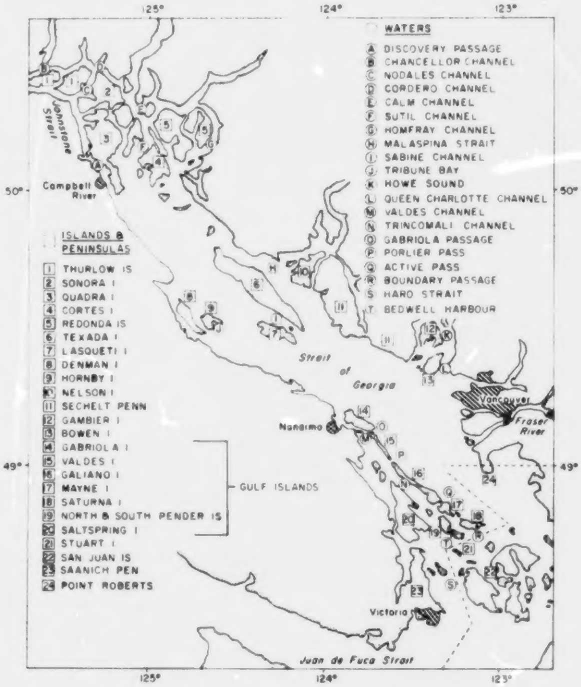
LAKE WASHINGTON
Issaquah River
Cedar River

FIG. 1. The waters around Vancouver Island, British Columbia, Canada, and the sockeye salmon nursery lakes and major spawning tributaries of the Fraser River system.

Attempts have been made to relate the changes in migratory behaviour of Fraser River sockeye to offshore oceanographic indices (Tully et al. 1960; Royal and Tully 1961; Favorite 1961) and to use the relationship to predict the proportion of fish that will take the northern route (Wickett 1977; IPSFC 1984; Hamilton 1985; Mysak 1986). However, none of these relationships has adequately explained the variation in migratory routes. The hypothesis tested in this study was that the route around Vancouver Island followed by adult sockeye salmon returning to the Fraser River is determined by the pathway previously followed as seaward migrating juveniles (Groot et al. 1984). The underlying assumption was that emigrating juveniles record sequences of environmental characteristics along the migratory route, and these are retraced during the homeward migration.

To reach the Pacific Ocean sockeye salmon smolts of the Fraser River system must swim either south and then westerly or north around Vancouver Island (Fig. 1 and 2). The actual routes are unknown, but it has been assumed that most Fraser River sockeye juveniles leave the Strait of Georgia south around Vancouver Island (Healey 1980).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Ⓔ CALM CHANNEL
Ⓕ SUTIL CHANNEL
Ⓖ HOMFRAY CHANNEL
Ⓗ MALASPINA STRAIT
Ⓘ SABINE CHANNEL
Ⓙ TRIBUNE BAY
Ⓚ HOWE SOUND
Ⓛ QUEEN CHARLOTTE CHANNEL
Ⓜ VALDES CHANNEL
Ⓝ TRINCOMALI CHANNEL
Ⓞ GABRIOLA PASSAGE
Ⓟ PORLIER PASS
Ⓠ ACTIVE PASS
Ⓡ BOUNDARY PASSAGE
Ⓢ HARO STRAIT
Ⓣ BEDWELL HARBOUR
ISLANDS & PENINSULAS
1 THURLOW IS
2 SONORA I
3 QUADRA I
4 CORTES I
5 REDONDA IS
6 TEXADA I
7 LASQUETI I
8 DENMAN I
9 HORNBY I
10 NELSON I
11 SECHELT PENN
12 GAMBIER I
13 BOWEN I
14 GABRIOLA I
15 VALDES I
16 GALIANO I
17 MAYNE I
18 SATURNA I
19 NORTH & SOUTH PENDER IS
20 SALTSPRING I
21 STUART I
22 SAN JUAN IS
23 SAANICH PEN
24 POINT ROBERTS
GULF ISLANDS
Johnstone Strait
Campbell River
Strait of Georgia
Nanaimo
Vancouver
Fraser River
Victoria
Juan de Fuca Strait

FIG. 2. The Strait of Georgia identifying the important islands, peninsulas, channels, passages, bays, and harbours.

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[1] In this paper "smolts" applies to sockeye salmon juveniles in the time between migration out of nursery lakes, and leaving inshore waters such as the Strait of Georgia and Juan de Fuca, Johnstone, and Queen Charlotte straits.

To examine whether there is a link between the migratory routes of the juveniles and the adults, we determined the migratory routes of sockeye salmon juveniles through the Strait of Georgia on their way to the Pacific Ocean, and we compared these with the pathways of the returning adults from the same and from other brood years on their way to the Fraser River.

Methods and Techniques

Information on the temporal distribution of juvenile sockeye in the northern and southern part of the Strait of Georgia was obtained by purse seining and two-boat trawling. Fishing operations were carried out during 1982–84 with three departmental research vessels, Caligus (28 tons net), Keta (16 tons net), and Tahlok (8 tons net). All boats used similar purse seine gear, with nets measuring from 275 m by 34 m for the largest to 210 m by 22 m for the smallest vessel. Mesh sizes of the bunt end varied from 6 mm ($^1/_4$ inches) to 12 mm ($^1/_2$ inches). Caligus could only fish in water deeper than about 30 m, while Keta and Tahlok could set in waters as shallow as 20–24 m. The latter two boats could work closer to shore, which was important because we found early in the study that sockeye smolts stay close to shore in many areas during their migration through the Strait of Georgia.

The trawl net measured 6.1 m wide by 3 m deep with an overall body length of 17.7 m and was constructed from 3 sizes of knotless netting; 50 mm and 25 mm stretched mesh in the body and 13 mm in the cod end. The net was towed between two boats at a speed of 5.5 km/h and each tow lasted about 10 minutes, covering a distance of approximately 1 km.

We abandoned the two-boat trawling technique in 1982 after 18 sets, since it caught appreciable numbers of chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) fry, which were dead at the end of the set. Purse seining allowed us to sort out the catch without harming the fish unduly and return to sea those not required for analysis.

All seine sets were carried out during daylight hours, usually between sunrise and noon, because early trials in 1982 indicated that fishing for juvenile sockeye was most successful during these times. Sets lasted about 10–30 min. The nets of Tahlok, Keta, and Caligus probably caught fish to depths of 15, 18, and 25 m, respectively. Echosounding records (Simrad Model EK 38) indicated that the targets were concentrated in the top 10 m of the water column in those areas where high numbers of sockeye juveniles were caught. A similar depth distribution of migrating sockeye smolts in saltwater was observed by Straty (1974) in the Bristol Bay area. We therefore assumed that we were usually fishing at the appropriate depth for juvenile sockeye and that the numbers caught per set gave a reasonable indication of concentration of fish per area.

Fishing in each of the 3 years of operation was carried out with two of the three research vessels. Generally, one boat operated in the southern and one in the northern part of the Strait of Georgia. In 1982, 94 purse seine and 18 trawl sets were made between May 11 and June 25. In 1983, 227 seine sets were made between May 2 and July 13, and in 1984, 272 seine sets were carried out from April 14 to July 4. A total of about 1 000, 10 000, and 15 000 juvenile sockeye salmon were caught in the 3 years, respectively. The surveys extended south to include the San Juan Islands region in 1983 and 1984.

The catch was sorted in live tanks on board each vessel. A maximum of 50 smolts/set were kept for further analysis.

Results

Catches of sockeye salmon smolts varied greatly among sets during the 3 years of operation (Groot et al. 1986). Figure 3 outlines the distributions of seine sets in the Strait of Georgia for 1982, 1983, and 1984 combined, in which more than 5, 40, and 80 smolts were captured per set. Two main distribution patterns of sockeye smolts are evident: one extending north of the Fraser River estuary along the mainland coast and a second one around the Gulf Islands and extending north through the Strait of Georgia towards Lasqueti and Texada islands. Both concentrations then continue north along the mainland coast into Sutil, Calm, and Cordero channels (Fig. 2 and 3). No smolts were found in Discovery Passage in our surveys, although Brown et al. (1984a and b) caught appreciable numbers during beach seining operations for coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) juveniles in this passage during 1984, but none in 1982 and 1983.

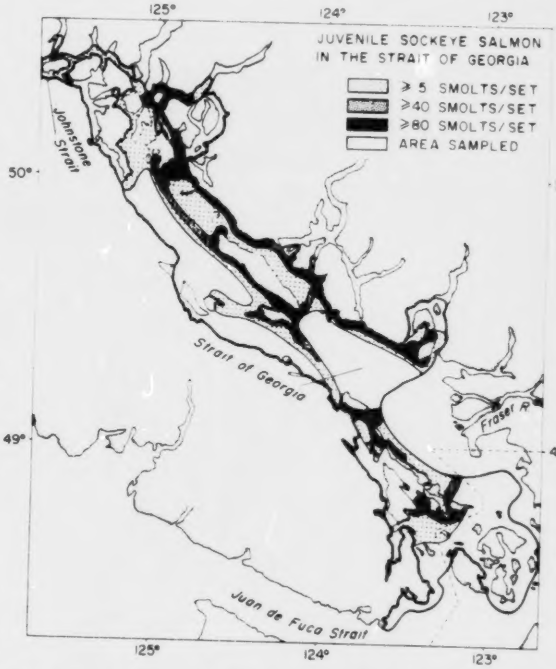

FIG. 3. The area sampled and the distribution of purse seine and tow-boat trawl sets for 1982, '83, and '84 combined, in which 5, 40, and 80 or more smolts were captured per set.

Only three smolts were captured among the San Juan Islands in American waters and along the southeastern shores of Vancouver Island in Juan de Fuca Strait. It is possible that we could have missed the movements of sockeye smolts through the San Juan Islands and Juan de Fuca Strait, (i) if they occured early in the season before our surveys started or (ii) if the sockeye smolts swam deeper in the southern waters and therefore escaped being captured. With respect to the first point, appreciable numbers of smolts were still caught among the Gulf Islands immediately prior to sampling among the San Juan Islands. Thus, if smolts were moving south around Vancouver Island towards the Pacific Ocean we should have caught at least some. In the case of the second point, sockeye smolts were caught with juveniles of chum, chinook, and coho salmon throughout this study. Because, we still caught the young of other Pacific salmon among the San Juan Islands, we do not think that we would have missed sockeye smolts had they been present.

We conclude that the distribution patterns of sockeye smolts during 1982—84 indicate that most smolts migrated out of the Strait of Georgia in a northern direction and moved through the eastern channels (Sutil and Calm channels) to Johnstone and Queen Charlotte straits towards the Pacific Ocean. This suggests that Fraser River sockeye smolts have a strong northward directional preference once they enter salt water.

We did not fish in the area off the Fraser mouth and Juan de Fuca Strait because others have collected information on distribution of juvenile Pacific salmon in this region before. Barraclough and Phillips (1978) used a two-boat trawl technique concentrating their efforts in the Fraser River plume area. Chapman (1970) surveyed the areas around the Fraser River outflow and the Gulf and San Juan islands using a small purse seine. Healey (1978, 1980) used both two-boat trawling and purse seining during his investigations of chum, coho, and chinook juvenile distributions in the Strait of Georgia with the same boats and nets used in this study. The Fisheries Research Institute staff at Seattle, Washington, sampled Juan de Fuca Strait, employing a large fine meshed seine (Dr. R. Burgner and Mr. C. Harris, pers. comm. Fisheries Research Institute, Seattle, Washington, USA; Hartt 1980 and Hartt and Dell 1986). As mentioned above, Brown et al. (1984a and b) did extensive beach seining in Discovery Passage during 1982–84.

We assumed that in all these investigations sockeye juveniles would have been caught had they been present in the areas of sampling. Combining the results of these studies with ours gives information on the progress of the migratory movements of juvenile sockeye salmon in the Strait of Georgia over two-week intervals between April 15 and June 30 (Fig. 4 A–E).

By the last two weeks of April sockeye smolts have started to move from the Fraser River into the Strait of Georgia (Fig. 4A). The distribution of fish extended in northwestern, western, and southern directions, with the highest concentrations of smolts in areas northwest and west of the river mouth.

During the first two weeks of May (Fig. 4B), sockeye smolts have primarily proceeded along the mainland coast as far as Texada Island (Malaspina Strait), but others have also moved across the Strait of Georgia toward the Gulf Island in westerly and southerly directions. The catch per set was highest in areas north and west of the Fraser River mouth. If the major tendency of the smolts is to swim northward after leaving the Fraser River, then the westerly movements toward the Gulf Islands can be interpreted as follows.

The Fraser River runoff peaks in early summer when melting rates of ice and snow fields in the interior of British Columbia are high. During periods of high Fraser River discharge a visible plume extends across the Strait of Georgia (Royer and Emery 1982). Between Point Roberts and Galiano Island surface currents can average 23 cm/s on flood and 43 cm/s on ebb, with maxima of 100 cm/s in each case (Pickard 1956). The momentum of river water flowing from the main arm, containing 75% of Fraser River runoff, causes it initially to be directed southwesterly toward the Gulf Islands. Strong tidal currents of 50 cm/s on normal tides pushes the plume to the south during an ebbing tide and west on a flooding tide (Thomson 1981; Bolton et al. 1983). Brett et al. (1958) indicated that smolts of the size (about 80 mm) and in the temperature range with which we are dealing are capable of sustained swimming speeds of 24 to 34 cm/s. Direct measurements of the actual speed of migrating schools made at Babine Lake showed mean speeds from 23 to 30 cm/s (Johnson and Groot 1963; Groot 1972). Because the swimming speeds of sockeye smolts are generally less than the flow in the Fraser River plume and the tidal currents, the assumed northerly directional tendency will be affected. We conclude therefore, that the westerly and southerly movements of smolts across the Strait of Georgia occur as a result of a combination of transport by the Fraser River plume and tidal currents rather than as a result of directed migration on the part of the fish.

Figure 4B also suggests that the smolts moved north along Valdes Island and through Gabriola Pass to Valdes Channel after reaching the Gulf Islands (Fig. 2). Strong tidal streams (up to 100 cm/s and more) occur in the passes, with ebb and flood tides pushing water out of, and into the Strait of Georgia, respectively (Thomson 1981). Smolts will certainly be transported through the passes if they accumulate near the entrances.

During the last two weeks of May the sockeye moving along the mainland coast reached the northern part of the Strait of Georgia and entered Calm and Sutil channels (Fig. 4C). The concentrations of fish were greatest close to the mainland shore. Some smolts moved a short distance into Howe Sound. This is probably a confusing area because water moves in and out with the tides at rates about 25 cm/s (Thomson 1981). Inlets farther up the coast were not sampled; thus, it is not known if the smolts in these places were diverted from their northern migration route. In the south the smolts moved through Active, Porlier, and Gabriola passes during the last two weeks of May and accumulated east of the Gulf Islands (Fig. 2 and 4C). Concentrations of smolts were also evident in an area adjacent to Roberts Point (Fig. 4C). As mentioned above, we assume that this is caused by strong tidal influences in this region. No smolts were captured among the San Juan Islands, despite the strong tidal currents (greater than 140 cm/s at maximum ebb) through Boundary Passage and Haro Strait. However, great concentrations (up to 2400 smolts per set) were found around the Pender islands, especially in Bedwell Harbour (Groot et al. 1986) (Fig. 2).

In early June the area off the Fraser River mouth was devoid of smolts (Fig. 4D), indicating that the downstream migration was over. In the north the smolts reached Johnstone

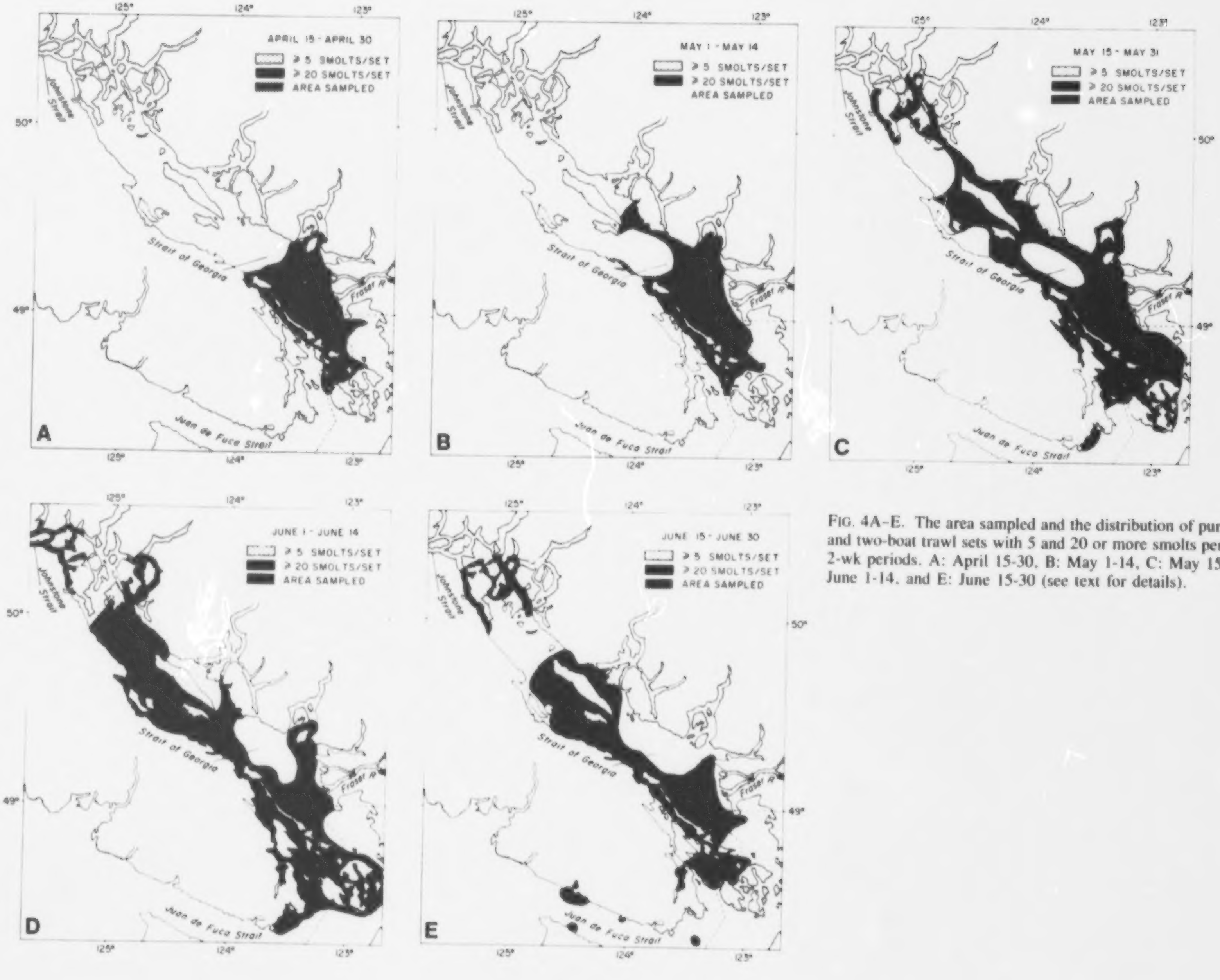
APRIL 15 - APRIL 30
MAY 1 - MAY 14
MAY 15 - MAY 31
JUNE 1 - JUNE 14
JUNE 15 - JUNE 30
≥ 5 SMOLTS/SET
≥ 20 SMOLTS/SET
AREA SAMPLED
Johnstone Strait
Strait of Georgia
Juan de Fuca Strait
Fraser R.
125°
124°
123°
50°
49°
A
B
C
D
E

FIG. 4A–E. The area sampled and the distribution of purse seine and two-boat trawl sets with 5 and 20 or more smolts per set per 2-wk periods. A: April 15-30, B: May 1-14, C: May 15-31, D: June 1-14, and E: June 15-30 (see text for details).

Strait through Chancellor and Nodales channels and they were also distributed through Homfray Channel (Fig. 2). In the southwest part of the Strait of Georgia they had accumulated west of the Gulf Islands, especially between and around North and South Pender Island. They had also moved north between Gabriola and Vancouver islands toward Lasqueti and Texada islands. Greatest concentrations occurred along west Texada Island and farther toward Cortes and Redonda islands (Fig. 2 and 4D). These smolts probably joined the last of the smolts that immediately moved north from the Fraser River mouth. There was also an indication of movement south along the east side of Saanich penninsula (Fig. 2 and 4D). The only appreciable catch of sockeye smolts in this area was a group of 70, made by Chapman (1970) near Victoria. These could have been swept south by the strong tidal currents running through Haro Strait. It is significant that no smolts were captured among the San Juan Islands, which supports the conclusion that the general tendency of these fish is to swim north.

By the last 2 weeks of June the smolts had left the area west of the Gulf Islands, with remnants passing Gabriola Island and moving northward toward Lasqueti and Texada islands (Fig. 4E). No sampling was done in northern Strait of Georgia during June (Fig. 4E) and thus it is not certain when the majority of smolts left these waters. About 29 smolts were caught near the entrance of Juan de Fuca Strait in seven sets (R. Burgner and C. Harris pers. comm. Fisheries Research Institute, Seattle, Washington, USA), indicating that some sockeye juveniles do leave the Strait of Georgia via the southern route. However, the numbers are small and some of these could have been of Lakes Washington, Ozette and Quinalt origin in Washington State, USA.

Discussion

The important finding of this study was that Fraser River sockeye salmon smolts leave the Strait of Georgia for the Pacific Ocean via the northern route through Johnstone and Queen Charlotte straits and not south via Juan de Fuca Strait (Fig. 5). This suggests that these smolts have a northward directional tendency as they enter salt water. Such direction finding capabilities have been shown by Groot (1965) and Quinn and Brannon (1982) for sockeye smolts migrating out of lakes. The smolts showed preferred directions under experimental conditons which were appropriate for reaching the lake outlet. In addition, Brannon (1972) and Quinn (1980) reported that sockeye salmon fry from two lake systems of the Fraser River, Chilko and Harrison lakes (Fig. 1), have built-in directional preferences corresponding to the long axis of the lakes.

The Fraser River system contains 50–60 separate sockeye salmon stocks which spawn in tributaries of about 22 nursery lakes (IPFSC 1954–86). Approximately 12 of the lakes are major sockeye producers and most of these have outlet waters flowing in a variety of compass directions (Fig. 1). Although the initial lake-exit-orientation of the smolts from the nursery areas of the different lakes must vary according to the compass directions of the respective outlets, their orientation must change to a northern to northwestern directional tendency by the time these fish reach the Strait of Georgia. Such a changing orientation over time has been shown by Groot (1965) for sockeye smolts from Babine Lake. Two populations from up-lake nursery areas shifted their directional preferences during emigration to a common compass direction appropriate to leave the lake. It is also possible that the change from fresh water to salt water releases the northward orientation. Whatever the mechanism, we assume that the directional tendencies of smolts of the Fraser River system change from a lake orientation to a northerly directed preference when they reach salt water.

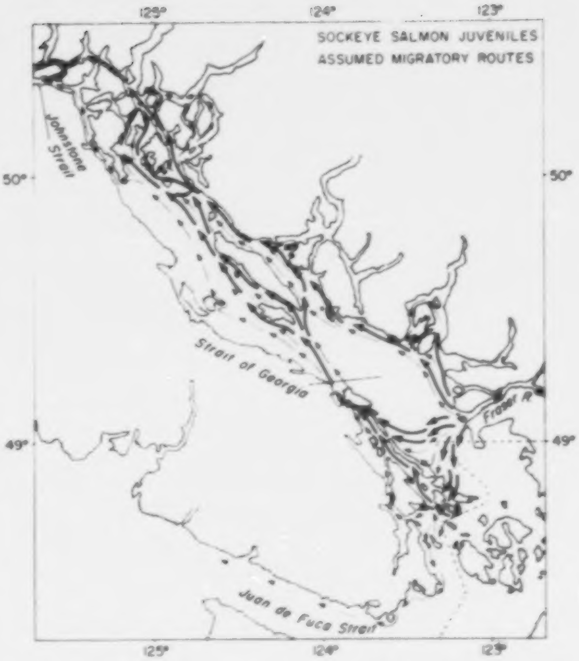

FIG. 5. The assumed migratory routes of Fraser River sockeye salmon smolts in the Strait of Georgia on their way to the Pacific Ocean.

The migratory directions of Fraser sockeye smolts in the Strait of Georgia are similar to those for juvenile Pacific salmon migrating in the North Pacific Ocean. Studies along the North American coast have shown that juvenile sockeye, pink, and chum salmon migrate northward along the Gulf of Alaska coast in a narrow band, less than 36 km wide off southeastern Alaska and increasing in width in northern areas of the Gulf as the continental shelf widens (Hartt 1980; Hartt and Dell 1986). The band of juvenile salmon is at least 1800 km long, extending from southern Vancouver Island to Yakutat in Alaska, and lasts about three months (Hartt 1980). This also strongly suggests that the general directional tendency of juvenile sockeye salmon is to move north after reaching salt water.

A north–northwesterly orientation will tend to concentrate the sockeye juveniles along the coastline of British Columbia and southern and central Alaska. Because of this tendency, we speculate that when these fish reach the tip of Vancouver Island they would cross over to the mainland shore and continue through the eastern portion of Queen Charlotte Sound and Hecate Strait. They may then reach the Pacific Ocean again through Dixon Entrance. Hartt (1980) and Hartt and Dell (1986) suggested this possibility, since they did not capture any sockeye juveniles between Vancouver and the Queen Charlotte islands, but did collect them along the southern coast of Alaska.

Sockeye salmon smolts seem to migrate rapidly through the Strait of Georgia. The distance from the Fraser River mouth to the northern part of the Strait is about 200 km. The migration of smolts from the Fraser River into the Strait of Georgia ended in late May (Fig. 4C and D). By the end of June most of these fish had left the Strait (Fig. 4E), which suggests that they take about 1 month to travel from the river mouth to the northern part of the Strait. Thus, the smolts need to travel at a rate of 6–7 km/d to cover the distance through the Strait of Georgia. Tagging studies by Johnson and Groot (1963) established similar migration rates (5–8 km/d) for sockeye smolts in Babine Lake. Swimming at the maximum sustained speeds of 24–34 cm/s (20.7–29.4 km/d) (Brett et al. 1958), the smolts would have had to travel from 5.3 to 7.5 hours a day on a direct course to pass through the Strait of Georgia in about 30 days. (see also Johnson and Groot 1963 and Groot 1972). In general, young sockeye salmon are not seen for very long in inshore waters and it is inferred that they move seaward rather quickly (Manzer 1956; Straty 1974).

How do the migratory routes of the juveniles and the adults compare? Sockeye salmon returning to the Fraser River from the ocean feeding grounds show substantial interannual variations in the proportions of fish travelling via the northern and southern routes around Vancouver Island (Fig. 1). The northern diversion rate has ranged from 2 to 80% (average 24%) during the last 33 years (IPSFC 1954–86). Thus, not all adults retrace the migratory routes of the juveniles during their return migration. This conclusion is strengthened by the 1984 and 1985 returning adults, which showed northern diversion rates of only 31% in both years (IPSFC 1985, 1986). These fish were followed in 1982 and 1983 as juveniles during their migration out of the Strait of Georgia and most left via the northern route. We therefore conclude that the hypothesis that the route around Vancouver Island of adult sockeye salmon returning to the Fraser River is determined by the pathways followed as seaward migrating juveniles 2 years previously (Groot et al. 1984), could not be substantiated.

The coastal approach route of adult Fraser River sockeye during the last 8–10 years were correlated with coastal sea surface temperatures (IPFSC 1984; Hamilton 1985; Mysak 1986; C. Groot unpubl. data). When conditions offshore were warmer than usual, sockeye salmon tended to approach the coast of British Columbia at the north end of Vancouver Island and continued to the Fraser River primarily through Queen Charlotte and Johnstone straits. When the Gulf of Alaska was colder, landfall usually occurred along the west coast of Vancouver Island and migration to the home river was primarily via Juan de Fuca Strait (Fig. 1). Thus, emigration of juveniles, which occurred, primarily, close to the coast of British Columbia and Alaska, was different from the return movements of the adults returning from the center of the Gulf of Alaska.

Griffin (1955) defined three types of orientation ability in animals. Type 1 is defined as a simple reliance on visual or other environmental land marks within familiar territory and as exploration or undirected searching in unfamiliar territory. Type 2, generally called compass or one-direction orientation, is the ability to move in a particular compass direction without reference to environmental marks. Griffin's Type 3, which is called bi-coordinate or goal orientation, refers to the ability of an animal to navigate towards a specific goal from an unfamiliar area. In general, type 2 orientation is performed by juveniles or young-of-the-year, which are migrating away from the breeding grounds for the first time. Goal orientation or navigation can apparently only be performed by older animals which have previous experience of the goal, i.e., wintering or breeding grounds (Perdeck 1958). The latter is often assumed to be the type of direction finding involved in homing. We conclude that the sockeye smolts appear to perform compass orientation (Griffin's Type 2) by moving in a north to northwestern direction upon entering salt water, whereas the adults show goal orientation (Griffin's Type 3) because they are able to locate the home river from either a northern or southern position dependent on where they make landfall in response to oceanographic conditons.

Acknowledgments

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Movements of Adult Sockeye Salmon (*Oncorhynchus nerka*) in British Columbia Coastal Waters in Relation to Temperature and Salinity Stratification: Ultrasonic Telemetry Results

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Abstract

QUINN, T. P., AND B. A. TERHART. 1987. Movements of adult sockeye salmon (*Oncorhynchus nerka*) in British Columbia coastal waters in relation to temperature and salinity stratification: ultrasonic telemetry results, p. 61–77. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

To understand better the factors influencing and guiding the migration of adult sockeye salmon (*Oncorhynchus nerka*) to the Fraser River, 17 salmon with ultrasonic transmitters were tracked between Vancouver Island and the mainland of British Columbia in summer 1985. Fish depth, determined by pressure sensors in 15 of the transmitters, was analysed in relation to vertical profiles of temperature and salinity recorded along the paths of the fish. The salmon were tracked in three distinct oceanographic regimes: cold, saline, weakly stratified waters of Queen Charlotte Strait and Johnstone Strait; less saline, vertically well-mixed waters of Discovery Passage; and warm, relatively fresh, strongly stratified waters of the Strait of Georgia.

Many salmon made deep dives immediately after release but ascended to the surface about 60–80 min later. Thereafter, individual fish established patterns of vertical movements that were essentially stable for the duration of the tracks (up to 14 h). In the northern (Queen Charlotte Strait and Johnstone Strait) and central (Discovery Passage) study areas, the salmon spent 69 and 64% of the time in the top 5 m of the water column after ascent from their initial dives (means = 5.5 and 7.0 m). In the Strait of Georgia, the salmon spent less time (21%) in the top 5 m (mean = 14.1 m). It appears that sockeye salmon had a general preference for near-surface water, as evidenced by their shallow distribution in the mixed region. In waters with more distinct vertical structure, they were often located at or near the depth where temperature and salinity gradients were largest. However, substantial variation in this pattern was observed, and the vertical distribution may reflect a combination of general depth preference and orientation to temperature and salinity stratification. Preference for stratified depths may be a mechanism for locating chemical stimuli guiding homing to the natal river.

Résumé

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Afin de mieux comprendre les facteurs qui influencent et déterminent la migration des saumons nerkas (*Oncorhynchus nerka*) adultes vers le fleuve Fraser, on a suivi les déplacements de 17 saumons munis de transmetteurs à ultrasons entre l'île de Vancouver et la côte continentale de la Colombie-Britannique à l'été 1985. La profondeur fréquentée, déterminée par des détecteurs de pression situés dans 15 des transmetteurs, a été analysée en fonction des profils verticaux de la température et de la salinité enregistrés le long du parcours du poisson. Les déplacements des saumons ont été suivis en fonction de trois régimes océanographiques : les eaux froides, salées et faiblement stratifiées du détroit de la Reine-Charlotte et du

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détroit de Johnstone; les eaux moins salées et bien mélangées verticalement du passage Discovery; et les eaux chaudes, relativement douces et très stratifiées du détroit de Géorgie.

Un grand nombre de saumons ont effectué des plongées profondes immédiatement après le lâcher mais sont remontés vers la surface 60–80 minutes plus tard. Par la suite, chaque saumon a établi un régime de déplacements verticaux généralement stables pendant toute la durée des relevés (jusqu'à 14 h). Dans les zones expérimentales septentrionale (détroit de la Reine-Charlotte et détroit de Johnstone) et centrale (passage Discovery), les saumons ont passé de 69 % à 64 % du temps dans les 5 m supérieurs de la colonne d'eau après la remontée suite aux plongées initiales (moyenne = 5.5 et 7.0 m). Dans le détroit de Géorgie, les saumons ont passé moins de temps (21 %) dans les 5 m supérieurs (moyenne = 14.1 m). Il semble que le saumon nerka préfère en général les eaux près de la surface comme le montre sa distribution dans les eaux peu profondes mélangées. Dans les eaux à structure verticale plus marquée, il était souvent présent à des profondeurs où les gradients de température et de salinité étaient les plus élevés, ou près de celles-ci. Toutefois, on a observé d'importantes variations de cette répartition; la distribution verticale peut traduire une combinaison d'une préférence générale pour une certaine profondeur et un déplacement vers une stratification de la température et de la salinité. Cette préférence pour des profondeurs stratifiées peut représenter un mécanisme de repérage des stimuli chimiques qui guident le retour vers les frayères natales.

Introduction

During late spring and summer, Pacific salmon (*Oncorhynchus* spp.) inhabiting the North Pacific Ocean and Bering Sea leave these waters and begin a complex migration that ends in their death on the spawning grounds. Hasler (1966) divided the migration into oceanic and riverine phases. Evidence generally indicates that the oceanic phase is well-oriented (Neave 1964; Royce et al. 1968; Quinn and Groot 1984; but see also Leggett 1977 for alternative interpretations). However, the factors initiating and guiding oceanic migrations are not well understood. Interannual variations in migratory timing and routes have been correlated with oceanic and coastal conditions (Burgner 1980; Hamilton 1985), but it is not clear how temperature or salinity patterns actually influence salmon (Groot and Quinn 1987). Once the salmon reach the mouth of their natal river, olfaction seems to be essential for identifying the stream which they left years earlier (Hasler and Scholz 1983). Coastal or estuarine waters represent the interface between oceanic and riverine environments, and as such may necessitate a transition from the guidance mechanisms used in the ocean to those used in rivers.

As the salmon migrate towards the mouth of their home river, they experience significant changes in oceanographic conditions throughout the water column, but they also begin to undergo the profound changes in morphology, physiology, and behavior that prepare them to enter freshwater and spawn. Thus physiological requirements may influence the immediate environment selected by maturing salmon. Since river runoff (containing homestream odors) contributes significantly to the oceanography of coastal waters, the water is also a potential source of guidance information. Moreover, the velocities of the tidal streams associated with near-shore waters (Thomson 1981) may equal or exceed the swimming capacity of adult salmon (Brett 1983) and thereby greatly help or hinder their horizontal movement.

To understand the mechanisms guiding homeward migrating salmon in general and the influences of temperature and salinity in particular, one must describe the movements of fish in relation to their immediate environment. Towards this end we tracked sockeye salmon, likely of Fraser River origin, with depth-sensing transmitters and concurrently recorded vertical profiles of temperature and salinity. Temperature was considered to be an important variable to monitor because oceanic temperatures show strong correlations with sockeye salmon route (IPSFC 1984; Hamilton 198[illegible] and timing (Burgner 1980; Blackbourn 1987). Salinity was monitored because it has been proposed as a mechanism guiding the seaward migration of smolts (McInerney 1964) and because it provides an indication of the distribution of river water in the estuary.

Materials and Methods

STUDY AREA AND SOCKEYE POPULATIONS

The waters between Vancouver Island and the British Columbia mainland have three regions with distinct oceanographic properties (Fig. 1). The Queen Charlotte Strait–Johnstone Strait region has cold, saline water with weak vertical stratification. The waters in Johnstone Strait become more horizontally and vertically homogeneous as one progresses eastward, and in the second region, Discovery Passage, the water is thoroughly mixed by remarkably strong tidal streams flowing through narrow channels and over shallow sills. For example, in Seymour Narrows between Quadra Island and Vancouver Island, peak tidal currents can exceed 25 km/h and exceeded 15 km/h on all but 6 days in July and August 1985 (Canadian Hydrographic Service 1985). The third region, the Strait of Georgia, is strongly stratified, warmer and much less saline than the waters in the northern or central regions. In the northern and central study regions, tides flood east and south, towards the Fraser River, as opposed to the northerly flooding tides in the southern region. The opposing floods meet in the northern Strait of Georgia, south and east of Cape Mudge.

The sockeye salmon used in this study were presumed to be returning to the Fraser River because (1) most southern B.C. sockeye originate in tributaries of the Fraser, (2) the populations from the west coast of Vancouver Island are not known to migrate on the east side of the island and (3) the route and timing of sockeye returning to the Nimpkish Lake system (which drains into northern Johnstone Strait from Vancouver Island) minimized our chances of sampling them (Gould and Stefanson 1985). Within the Fraser, there are many distinct spawning populations. The staff of the International Pacific Salmon Fisheries Commission are able to determine the likely origin of Fraser River sockeye salmon from scale pattern analysis (Henry 1961). They were able to make such determinations for some of the salmon tracked in 1985 (Table 1), but for the others the scales were lost or unreadable.

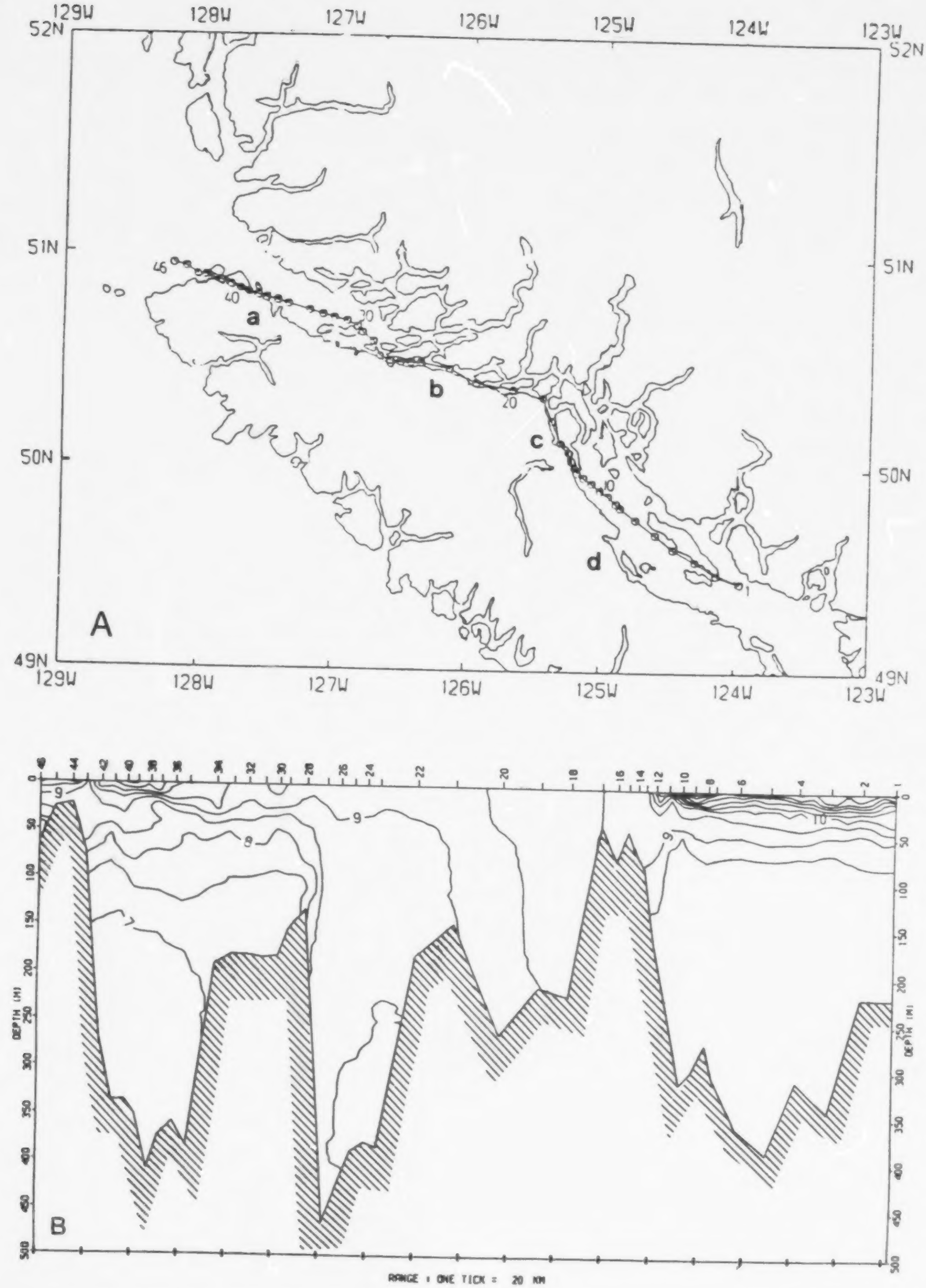

129W
128W
127W
126W
125W
124W
123W
52N
51N
50N
49N
46
40
30
20
10
1
a
b
c
d
A
DEPTH (M)
9
8
7
10
B
RANGE : ONE TICK = 20 KM

FIG. 1. Results of a baseline survey to determine the physical characteristics of the waters between Vancouver Island and the mainland. A) Cruise track of the CSS *Vector* June 24–25, 1985, showing stations numbered 1–46 where CTD casts were made (a = Queen Charlotte Strait, b = Johnstone Strait, c = Discovery Passage, d = Strait of Georgia); B) Thermal structure derived from the June 24–25 cruise. Station numbers correspond to those shown in the cruise track.

Table 1. Sex, age, fork length and tentative stock origin of sockeye salmon tracked in 1985. Age and stock identifications were made by the IPSFC. Sexes assessed externally in the field prior to release are designated with a "?". A slash (/) indicates that the scale was lost or unreadable, or that the sex could not be determined externally.

Fish	Sex	Age	Length (cm)	Population
8501	/	4	64	Stuart Lake (early)
8502	/	/	57	/
8503	/	/	65	/
8504	/	/	68	/
8505		4	63	Gates Creek
8506	/	/	65	/
8507		5	63	Bowron R., Raft R., or Fennell Cr.
8508	/	4	64	Horsefly R.
8509	r	5	70	Chilko R.
8510	/	4	64	Horsefly R.
8511	r	4	63	Horsefly R.
8512	/	4	62	Horsefly R.
8513	?	4	62	Horsefly R.
8514		4	61	Horsefly R.
8515	/	/	67	/
8516	r ?	4	67	Weaver Cr. or Portage Cr.
8517	r ?	4	63	Adams R. – Lower Shuswap R. or Horsefly R.

TAGGING AND TRACKING

The general research method was to capture a sockeye salmon, attach a transmitter to it, track its vertical and horizontal movements, and determine the vertical profiles of temperature and salinity along its track. Salmon were captured by the commercial purse seine vessel *Sea Luck*, in the waters between Vancouver Island and the mainland of British Columbia from July 4 to August 23, 1985 (Fig. 2). Typically, *Sea Luck* would complete a set by about 0600 h (PST). While the net was still in the water, four to six sockeye salmon would be transferred to a 1 m diameter live tank on the tracking boat, *Melibe*. A salmon was selected for tracking based on generally healthy appearance and large size to reduce the stress of transmitter insertion (mean fork length = 64 cm, Table 1). The fish was anesthetized with MS-222 (tricaine methanesulfonate) and a cylindrical ultrasonic transmitter was inserted into the stomach. Stomach insertion was chosen because it seems to be less traumatic than external attachment or surgical implantation (Mellas and Haynes 1985). The transmitters were 74 mm × 16 mm and weighed 28 g in air (13 g in water). They emitted pulses at one of five frequencies (50, 60, 65.5, 69 or 76.8 kHz) and the interval between pulses was directly proportional to water depth in 15 of the transmitters (Vemco, Ltd., Nova Scotia). Calibration of transmitters to a depth of 50 m prior to implantation in salmon indicated accuracy to ±1 m. The fish was then measured, tagged with plastic Petersen discs in the muscle below the dorsal fin and a scale was removed for analysis. The other fish were also anesthetized, measured and tagged. The salmon regained their equilibrium and commenced apparently normal swimming within 5 min of transfer to the recovery tank but were allowed at least 30 min before release. The tagged fish were released together, near the capture site unless sea conditions mandated release in a more protected site nearby. Upon release the fish were tracked with a directional hydrophone and receiver/decoder (Vemco Ltd.). The decoder provided a digital readout of depth, which was recorded every minute or as often as reception permitted. Because the transmitter range was generally only 100–200 m, the position of the boat closely approximated the position of the fish. Horizontal position, recorded at least every 5 min, was determined by Loran C (Raytheon Inc., Raynav 550) on the tracking boat, periodically calibrated using radar and local landmarks.

The tracking boat was followed by a self-propelled 12 m barge, *Nitinat Queen*, carrying the oceanographic equipment. A Guildline Model 8705 digital conductivity, temperature and depth (CTD) probe and a model 87102 control unit determined salinity and temperature as the probe was lowered through the water column. CTD casts were made along the fish's path at 15–30 min intervals. The profiles extended from the surface to 60 m or within 10–15 m of the bottom if the water was less than 60 m deep. We analysed the movements of the fish in relation to temperature and salinity, but profiles of density paralleled those of salinity (changes of 5°C and 1‰ salinity result in the same change in sigma t units). Current speed and direction were estimated from the movements of passive window blind drogues tracked by radar. Five sockeye salmon with depth sensing transmitters were tracked in each of the three oceanographic regions between Vancouver Island and the British Columbia mainland, and two others were tracked with position-only transmitters in the third region (Fig. 2).

Results

HORIZONTAL MOVEMENTS

The 17 sockeye salmon were tracked for a total of 115.77 h. During the tracks, some made substantial progress over the ground towards their presumed destination, the Fraser River. However, some fish moved very little and others did not swim towards the Fraser River. For each fish, net and gross movements were calculated from Loran readings taken at least every 5 min. The net movement of a fish represents the direction and shortest water distance from the point of release to the point where the fish was lost

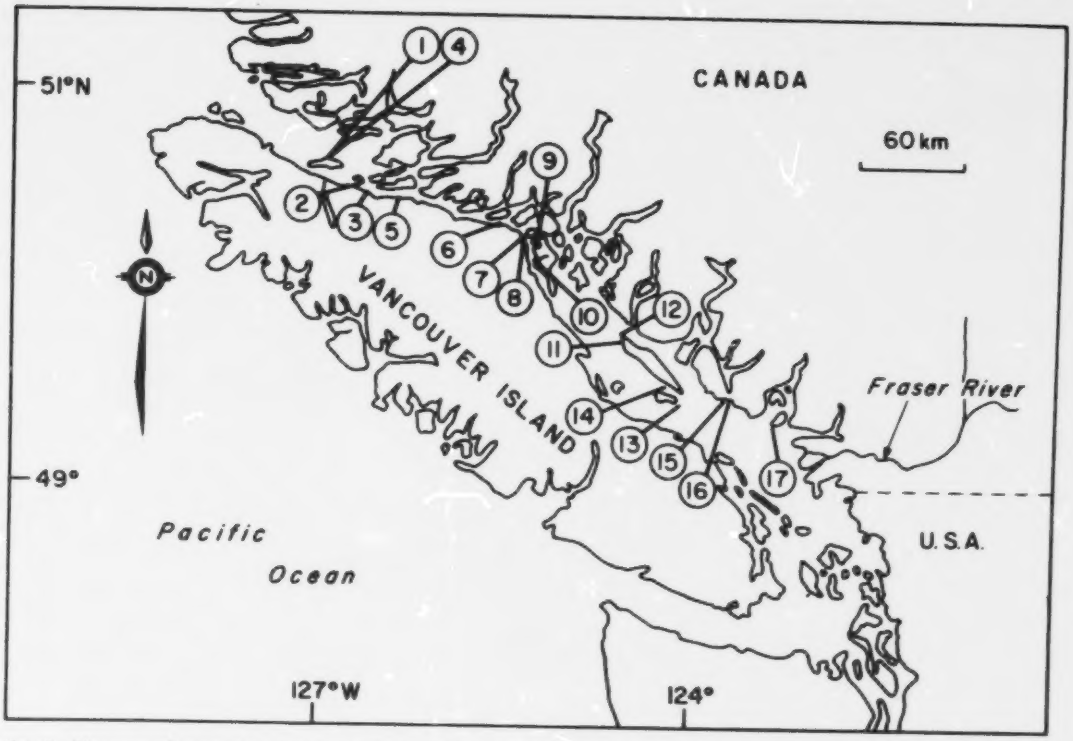

51°N
49°
127°W
124°
CANADA
60 km
N
VANCOUVER ISLAND
Pacific Ocean
Fraser River
U.S.A.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

FIG. 2. The area where sockeye salmon tracking took place, indicating the locations where the 17 salmon were released.

TABLE 2. Horizontal movements of 17 adult sockeye salmon tracked between Vancouver Island and the British Columbia mainland in 1985. Distances are expressed in km, direction is in degrees relative to geographic north. Mean direction is the unweighted mean of net directions of the fish.

Fish	Date	Duration (h)	Net km/h	Net direction	Gross km/h	Net/Gross ratio
8501	4 July	1.23	1.59	15°	1.84	0.86
8502	11	1.87	2.60	114°	3.38	0.77
8503	13	14.83	0.91	101°	1.52	0.60
8504	18	9.45	0.05	63°	1.43	0.03
8505	19	6.02	0.41	20°	1.60	0.26
8506	25	1.70	1.69	69°	2.53	0.67
8507	26	3.57	0.42	136°	2.38	0.18
8508	26	2.93	0.68	2°	2.60	0.26
8509	1 Aug.	12.33	0.18	212°	3.72	0.05
8510	2	4.98	0.89	195°	2.30	0.39
8511	7	7.83	1.59	299°	2.00	0.80
8512	8	10.00	0.12	111°	1.33	0.09
8513	15	2.93	2.19	125°	2.56	0.86
8514	16	9.82	1.34	112°	2.91	0.46
8515	17	7.02	2.30	110°	2.88	0.80
8516	22	12.50	2.72	108°	3.69	0.74
8517	23	6.75	1.15	274°	1.98	0.58
Means		6.81	1.22	97°	2.39	0.49

or recaptured. The gross movement is the estimated total distance that the fish swam while tracked. Net movement divided by the gross movement provides a rough indication of the directedness of the fish's movements. Net movements for the 17 fish ranged from 0.05 to 2.72 km/h ($\bar{X}$ = 1.22, Table 2). Gross movements averaged 2.39 km/h (range = 1.33–3.72). These swimming speeds are relative to the ground, and do not take into consideration the currents which in some cases approximated or exceeded the speed of the fish. The unweighted mean direction of net movement was 97°. If the net directions of the fish are weighted for duration of the track and for net/gross ratio, the mean direction is 111°. Using Moore's (1980) modification of the Rayleigh test for directional data, the mean bearing is marginally different from random ($0.10 > P > 0.05$).

The current patterns, as indicated by drogue movements, were very complex and were not quantitatively assessed in this study. However, it was evident from general drogue movements and our need to keep the tracking boat in gear that the salmon rarely drifted but were swimming almost constantly. Only one fish, 8512, spent a large amount of time with no apparent movement.

VERTICAL MOVEMENTS

Immediately following release, 10 of the fish made steep dives with an average duration of 79 min before abruptly ascending to within 5 m of the surface. Thereafter, these fish's patterns of vertical movement were largely unchanged for the remainder of the tracks. Four fish did not dive, and one was lost as it was ascending, apparently at the end of a dive (Table 3). Because the dives were not characteristic of the overall patterns of vertical movements (see Fig. 3, 4 for representative examples), they were omitted from calculations of mean depths.

Of the five sockeye tracked in the northern region (Nos. 8501–8505 in Fig. 2), three were tracked for sufficient periods to establish patterns of vertical and horizontal movements. The average post-dive depth was 5.5 m and virtually no time was spent below 30 m. Two of these fish (Nos. 8503 and 8505) spent over 80% of their post-dive time in the top 5 m (Fig. 5). Both of these fish were tracked in Johnstone Strait waters with weak thermal gradients. While the vertical movements of these two fish were similar, their horizontal movements differed greatly. No. 8503 was released-near the end of an ebbing tide and it milled around for 135 min before crossing the strait, travelling north and east along a flooding tide rip. It then circled in a back eddy for 165 min before moving east along the shore, then SE into mid-strait and east in the middle of the strait (Fig. 6). Most of this fish's progress was made into an ebbing tide. Fish No. 8505 was released 18 km east of No. 8503's release point along the south shore of the strait. It crossed the strait swimming at right angles to a weakly ebbing tide. It then swam west, into a flooding tide on the north shore, making no net progress in the last 4 h of the track. Fish No. 8504 was released north of Malcolm Island in Queen Charlotte Strait. It spent less time (45%) in the top 5 m but did not occupy deeper water than the other two (Fig. 5). This fish was tracked in water with a greater thermal gradient and a broader thermocline than the other fish had experienced. While it made virtually no net progress, tidal currents at this location were flooding generally SE at speeds averaging 2 km/h and occasionally reaching 4.5 km/h as inferred from drogue movements. Thus the fish must have been swimming steadily NW in order to maintain position relative to the ground.

Because the vertical patterns of temperature and salinity in Discovery Passage were essentially homogeneous, the depth preferences of sockeye salmon in this region may be considered to be independent of those variables. Water temperatures in this region ranged from 10.0 to 10.3° and

TABLE 3. Summary of the vertical movements of sockeye salmon tracked between Vancouver Island and the British Columbia mainland in 1985.

	Dive		Post-dive		
Fish	Duration (min)	Max. depth	Mean depth	S. D.	Max
8501[a]	74 +	27 ?			
8502[b]	no dive		12.4	12.7	40
8503	86	34	4.2	5.3	31
8504	70	25	7.9	6.2	30
8505	85	40	4.4	5.0	33
8506[b]	49	75	13.4	9.9	37
8507	80	54	9.3	9.9	53
8508	66	68	3.8	4.2	23
8509	75	70	6.9	8.8	38
8510	68	36	8.0	7.0	32
8511	122	39	17.3	10.8	44
8512	88	56	20.4	7.9	43
8513	no dive		6.7	4.8	18
8514	no dive		11.3	7.5	36
8516	no dive		14.9	5.1	29

[a] Fish lost when apparently ascending from dive.

[b] Very limited post-dive data on Nos. 8502 and 8506.

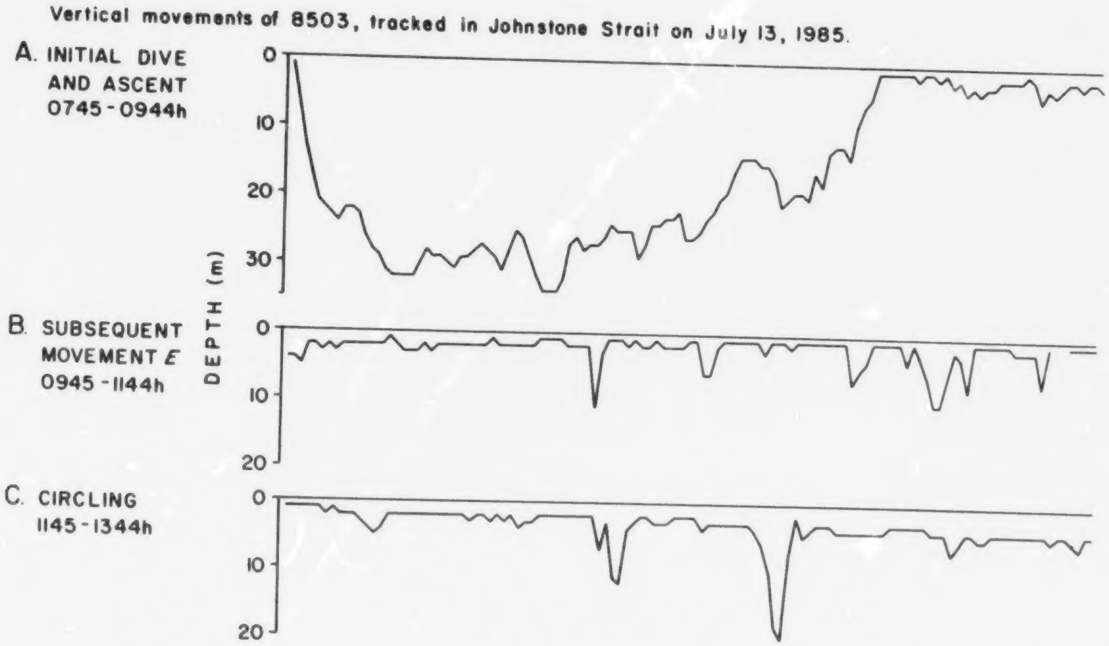


FIG. 3. Minute-by-minute record of the vertical movements of sockeye salmon No. 8503 showing initial dive and subsequent surface-oriented distribution.

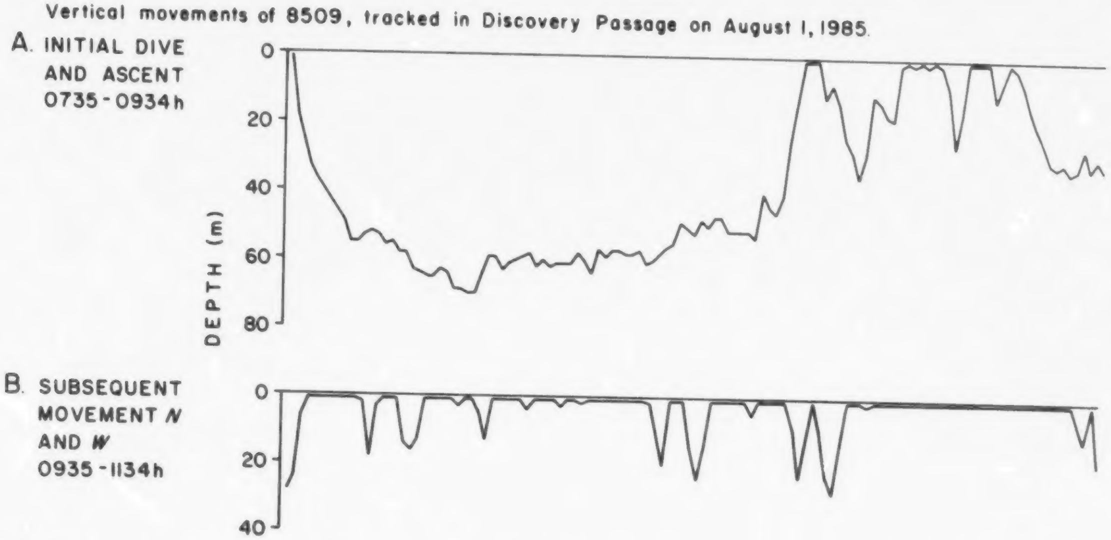


FIG. 4. Minute-by-minute record of the vertical movements of sockeye salmon No. 8509 showing initial dive and subsequent surface-oriented distribution.

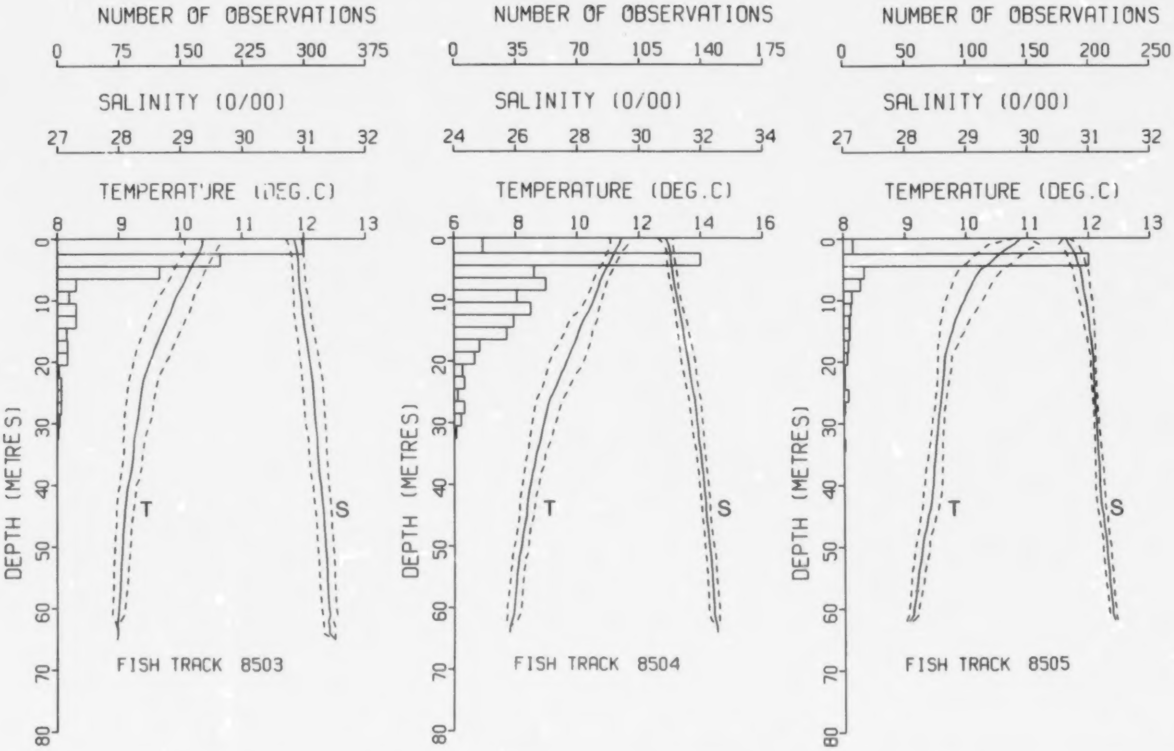


FIG. 5. Summaries of the depth distributions of three sockeye salmon tracked in the Queen Charlotte Strait–Johnstone Strait region in relation to the vertical profiles of temperature and salinity recorded along the paths of the salmon (solid line = average, dashed line = 1 S. D.). Each observation corresponds to 1 min of tracking.

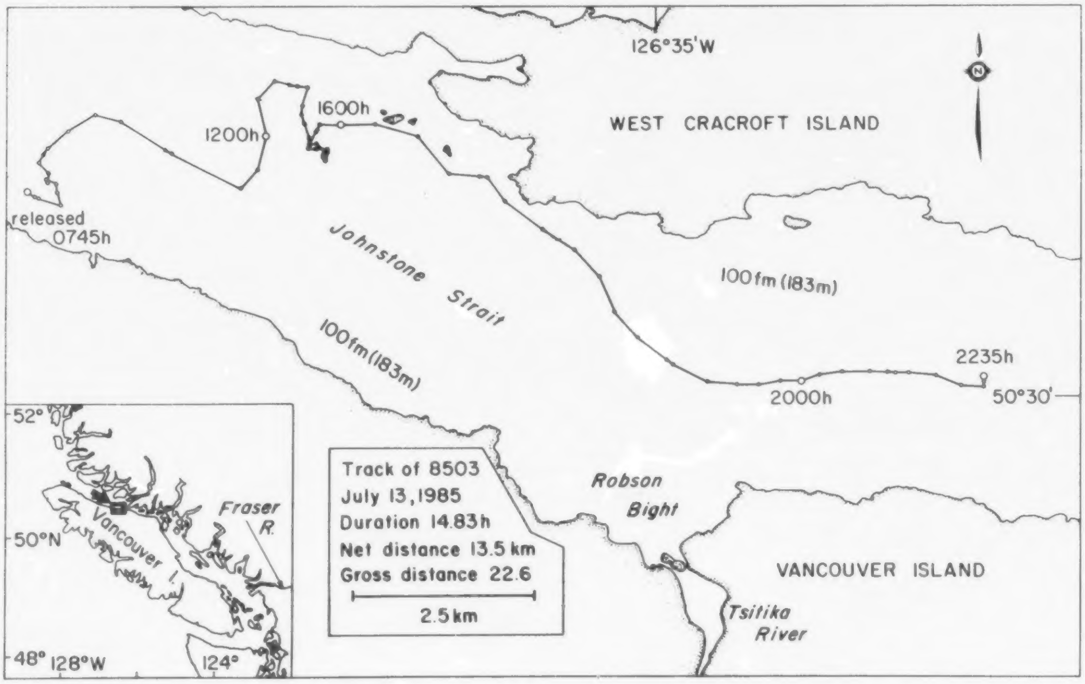

126°35'W
N
WEST CRACROFT ISLAND
1600h
1200h
released
0745h
Johnstone Strait
100fm (183m)
100fm (183m)
2235h
2000h
50°30'
Robson Bight
VANCOUVER ISLAND
Tsitika River
52°
Fraser R.
Vancouver I.
50°N
48°
128°W
124°
Track of 8503
July 13, 1985
Duration 14.83h
Net distance 13.5 km
Gross distance 22.6
2.5 km

FIG. 6. The horizontal movements of sockeye salmon No. 8503 in Johnstone Strait, plotted at 15 min intervals.

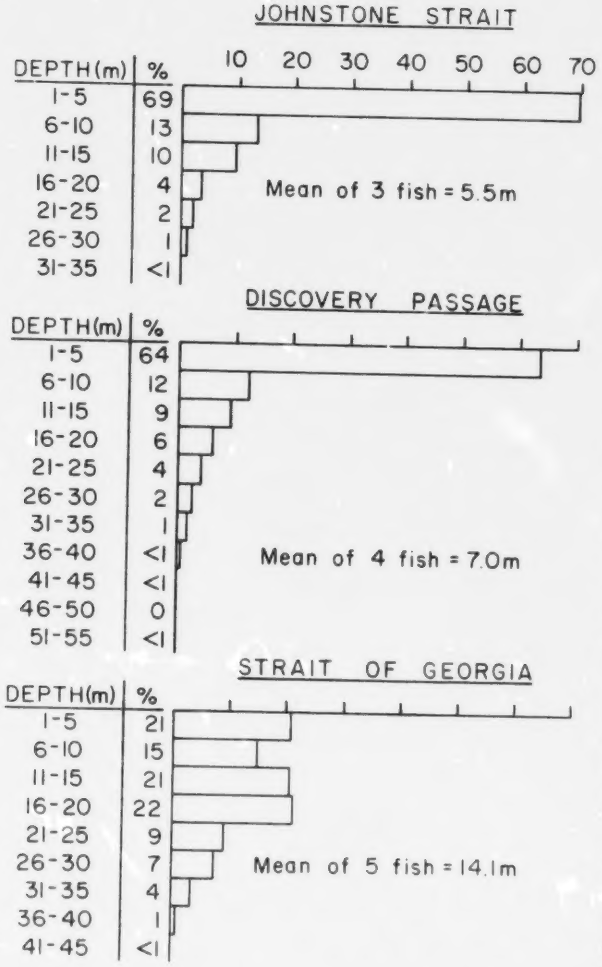


FIG. 7. Summary of the vertical distributions of three sockeye salmon tracked in Queen Charlotte Strait and Johnstone Strait, four in Discovery Passage and five in the Strait of Georgia. Bar graphs depict the average amounts of time spent by fish from the three different regions in 5 m depth increments.

salinities ranged from 29.8 to 30.6‰. However, at many CTD stations there were no detectable changes in temperature or salinity over the depth range examined. The average depth distribution of the four fish with sufficient data for analysis (Nos. 8507, 8508, 8509, 8910; Fig. 7) was similar but slightly deeper (mean = 7.0 m) than that of the three sockeye in the northern region. The four fish ranged from very surface-oriented (82% of the time in the upper 5 m for No. 8508) to somewhat deeper for the others: 67, 54, and 52% in the upper 5 m for Nos. 8509, 8507, and 8510; Fig. 8). One feature that distinguished the behavior of sockeye salmon in Discovery Passage from those in the northern region was the deepness of their initial dives. None of the fish in the north dove below 40 m, yet the first four sockeye released in the central region dove to 75, 54, 68, and 70 m. The fifth fish was released in a bay which may have limited its diving.

The horizontal movements of the salmon in this homogeneous region were more variable than their vertical distributions. No. 8507, released during a flooding tide, alternated active swimming into the tide with drift. In spite of the rapidly flooding tide in the area, the fish only travelled at a net speed of 0.42 km/h. No. 8508 was released during an ebb tide and spent much of its time holding position in back-eddies or actively swimming against the tide in mid-channel. No. 8509 was released off the NW corner of Quadra Island on an ebbing tide (Fig. 9). It moved away from the island, swimming into the tide and apparently drifting in back-eddies. It then swam north with the tide and west to Vancouver Island. It circled very close to shore, then swam rapidly south and southeast to the NW tip of Quadra Island, passing its release point. It continued south, swimming in southward-flowing water (though the water along the nearby shore was flowing rapidly north). After it subsequently swam north, this fish achieved virtually no net progress, even though it averaged 3.72 km/h over more than 12 h. Interestingly, on 6 occasions in the last 2 h of the track, a number of salmon were seen jumping in the immediate vicinity of the telemetered fish. Jumping was only observed when our fish was in the top 2 m, and never when it descended to about 20 m, as it often did during this period. When the fish was recaptured by *Sea Luck*, 58 other sockeye were captured with it, even though the net was set rapidly and at a site not known as a productive fishing area.

The last fish tracked in the vertically well-mixed oceanographic region was released in Deepwater Bay on Quadra Island at the end of an ebb tide. The water in the bay was still, and the fish circled inside for almost 2 h before swimming west and encountering the tide flooding south. It swam into the tidal current, but occasionally drifted southward. Ten min before the tide was predicted to reach a peak of 25 km/h 2.8 km away at Seymour Narrows, the fish turned and swam south with the tide. After 15 min, the fish's ground speed exceeded 7 km/h. It then turned and headed into the tidal current, backing downstream. It encountered a back-eddy and made northward progress in slack water along shore, even though the water in the middle of the narrows was moving at approximately 15–20 km/h. The fish was lost in the turbulence of the eddies and subsequently caught by a fisherman south of Texada Island in the Strait of Georgia.

Five salmon with depth transmitters were tracked in the Strait of Georgia. The depth-frequency distributions of these fish varied considerably. Two of the fish were surface-oriented (Nos. 8513 and 8514), two spent most of their time between 10–20 m (Nos. 8512 and 8516) and one (No. 8511) had a bimodal depth-frequency distribution with modes at the surface and at approximately 20–30 m (Fig. 10 A). One of the surface-oriented salmon, 8513, was tracked southeast of Lasqueti Island, moving steadily ESE until electronic failure ended the track. The fish almost never went below 16 m (Fig. 10 C) and spent large amounts of time at 1–4 m and 9–15 m. Fish 8514 was released in Sabine Channel, between Texada and Lasqueti islands. This salmon initially swam west (away from the Fraser River) into an ebbing tide that would have facilitated transport southeast towards the river. About 100 min later, the fish turned and swam east with the ebbing tide. It then swam back and forth in the channel before heading southeast into a flooding tide. In Sabine Channel, the fish experienced temperature gradients of approximately 0.21°C m^{-1} from the surface to 20 m. Below 20 m, temperatures declined gradually to about 9°. In the

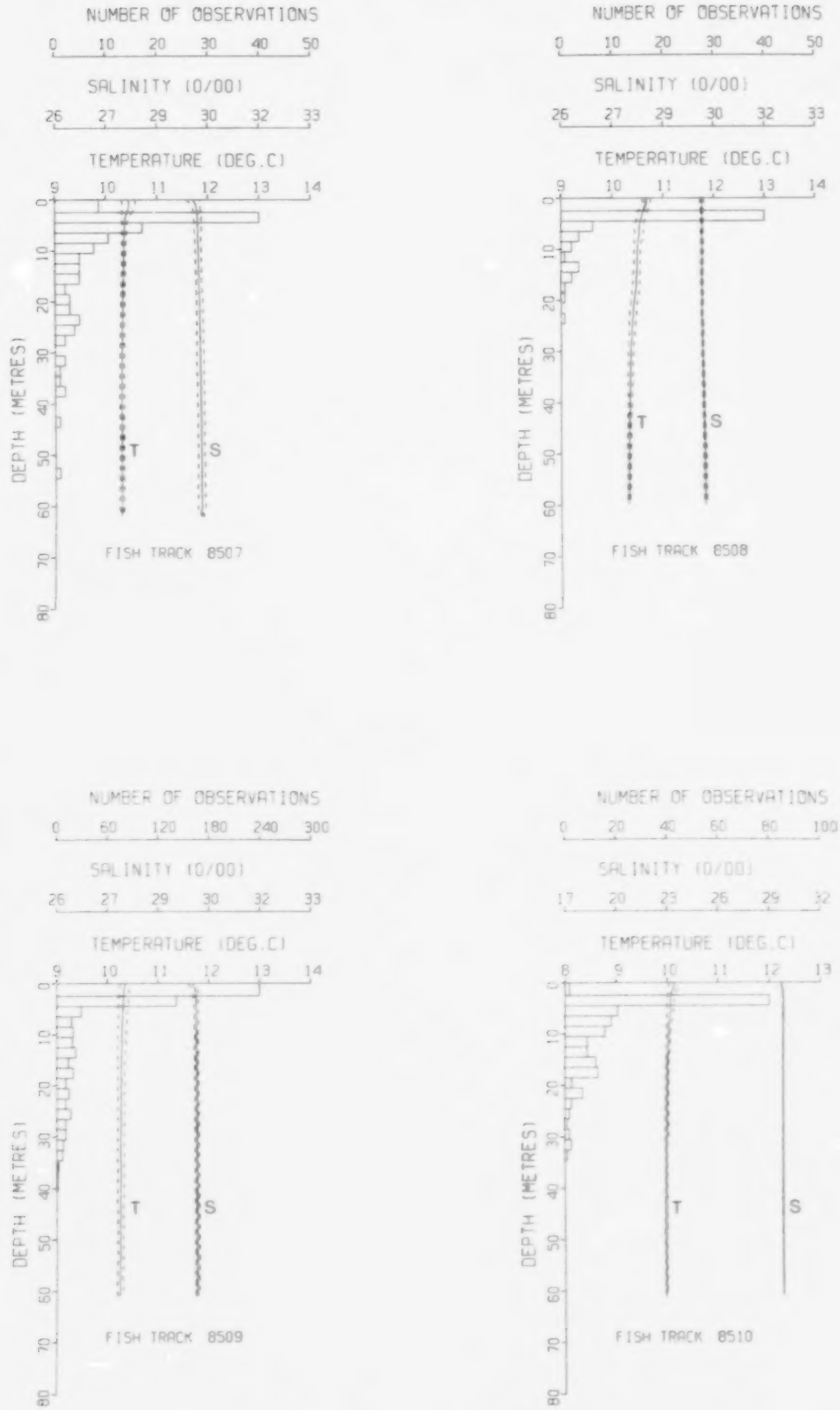


FIG. 8. Summaries of the depth distributions of four sockeye salmon tracked in Discovery Passage in relation to the vertical profiles of temperature and salinity recorded along the paths of the salmon (solid line = average, dashed line = 1 S. D.). Each observation corresponds to 1 min of tracking.

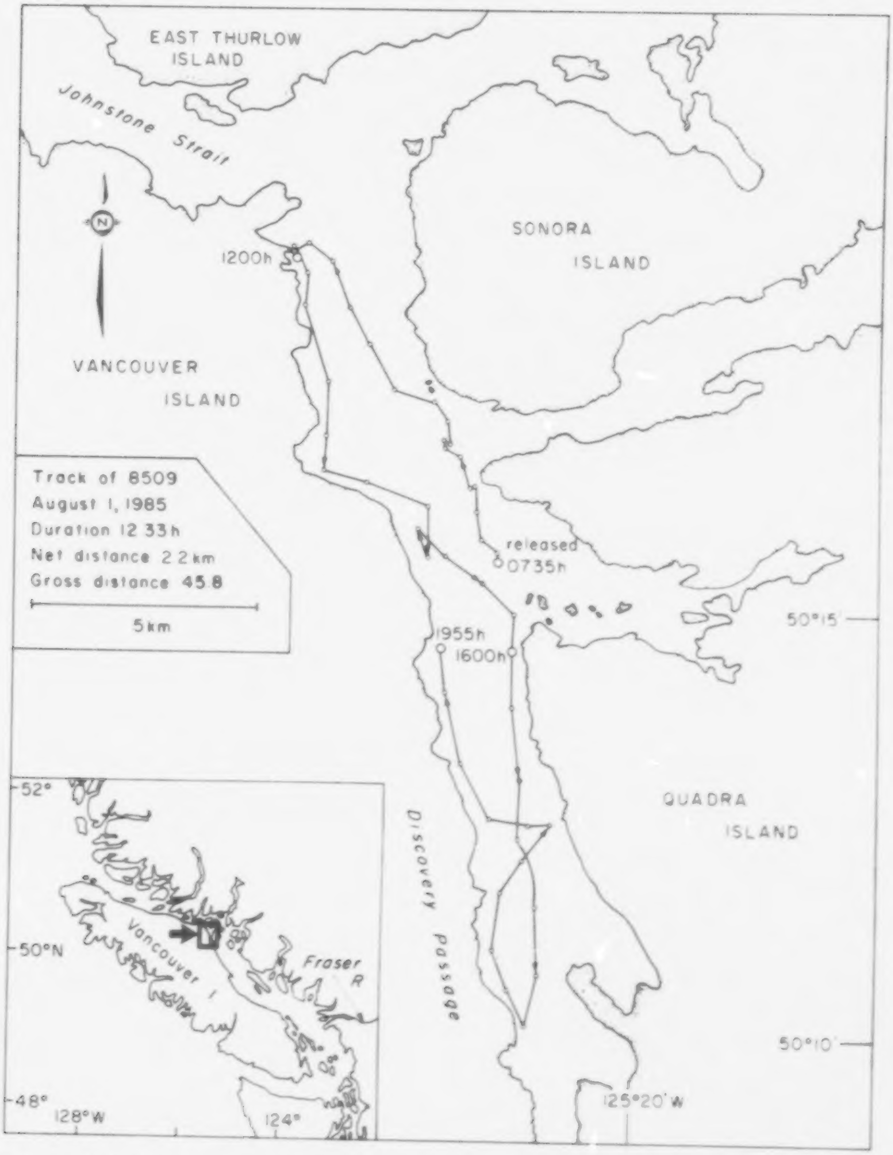

EAST THURLOW ISLAND
Johnstone Strait
N
SONORA ISLAND
1200h
VANCOUVER ISLAND
Track of 8509
August 1, 1985
Duration 12.33h
Net distance 2.2 km
Gross distance 45.8
5 km
released 0735h
1955h
1600h
50°15'
QUADRA ISLAND
Discovery Passage
50°10'
125°20'W
52°
50°N
48°
128°W
124°
Vancouver I
Fraser R

FIG. 9. The horizontal movements of sockeye salmon No. 8509 in Discovery Passage, plotted at 15 min intervals.

open water southeast of Sabine Channel, the surface waters were warmer (16–19°) and a gradient of about 0.41°C m^{-1} to 20 m was present. The salmon made numerous excursions between the surface and 15–20 m depths but spent little time below 20 m (Fig. 10 D). Thus the fish spent most of its time at the thermocline. Its horizontal movements took it ESE in open water, virtually repeating the route taken by 8513 the previous day, before it subsequently turned NE towards the mainland.

Considerable data are available for the two fish with depth distributions centered between 10 and 20 m. No. 8512 was tracked for 10 h but its net movement was only 1.17 km (Table 2). This fish was tracked in waters with strong vertical stratification and a pronounced two layer thermal structure. A layer of uniformly warm, brackish water in the top 8 m was separated from a layer of cold, relatively saline water from approximately 18 m to the bottom by a shallow distinct thermocline. The fish thus spent most of its time at or below the region of the largest gradients.

Salmon No. 8516 occupied a narrow depth range, spending 51.1% of its time between 16 and 20 m (Fig. 10 E). After release off the mainland approximately 45 km from the north arm of the Fraser River, this fish quickly established a pattern of rapid, directed swimming SE about 2–3 km from the shore (Fig. 11). It subsequently turned abruptly north and spent about 2 h swimming among the small islands that dot outer Howe Sound. The fish left the sound and resumed swimming in a virtually straight line towards the Fraser River. It once again began circling near the mouth of Burrard Inlet north of the Fraser River. The periods of highly

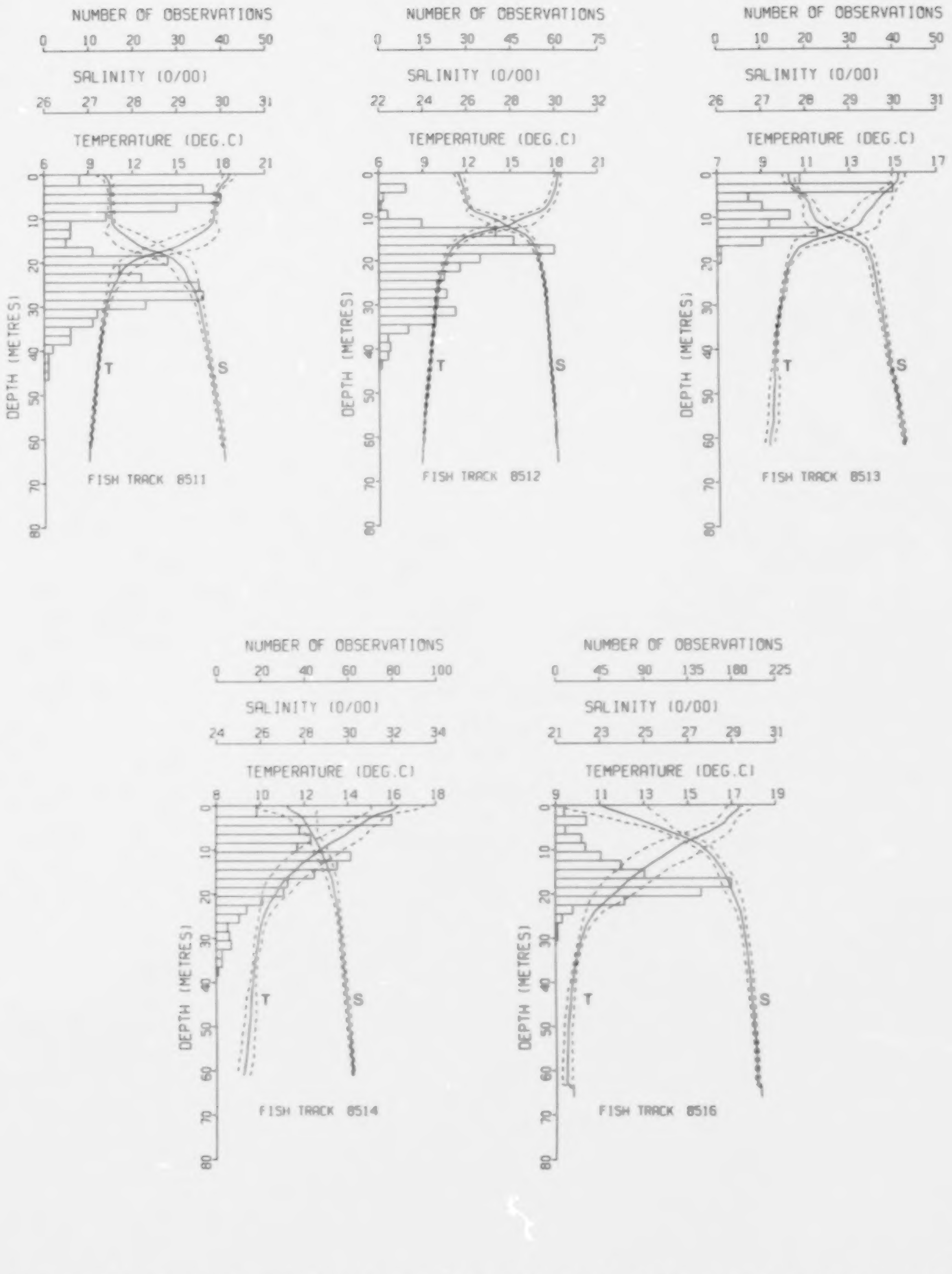
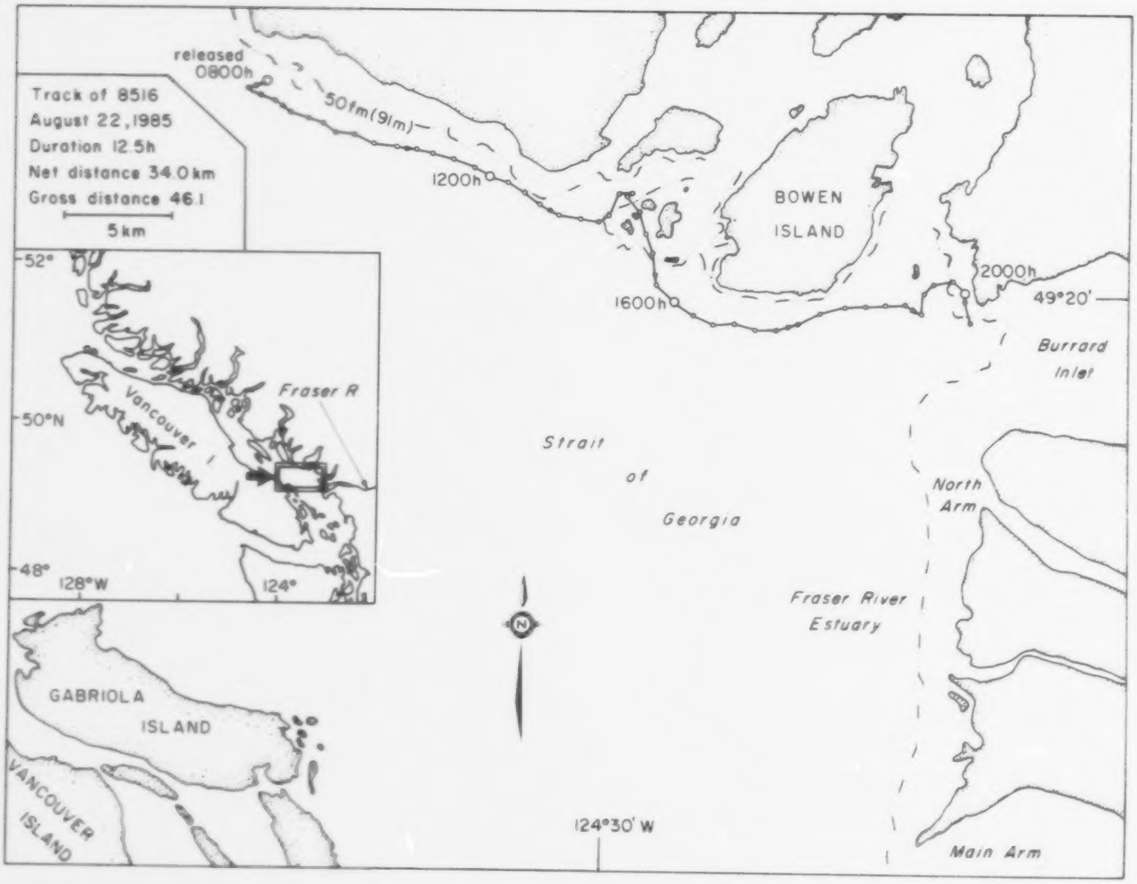


FIG. 10. Summaries of the depth distributions of five sockeye salmon tracked in the Strait of Georgia in relation to the vertical profiles of temperature and salinity recorded along the paths of the salmon (solid line = average, dashed line = 1 S. D.). Each observation corresponds to 1 min of tracking.



released
0800h
50fm(91m)
Track of 8516
August 22, 1985
Duration 12.5h
Net distance 34.0 km
Gross distance 46.1
5 km
1200h
BOWEN
ISLAND
2000h
49°20'
1600h
Burrard
Inlet
52°
Fraser R
50°N
Vancouver I
48°
128°W
124°
Strait
of
Georgia
North
Arm
Fraser River
Estuary
N
GABRIOLA
ISLAND
VANCOUVER
ISLAND
124°30' W
Main Arm

FIG. 11. The horizontal movements of sockeye salmon No. 8516 in the Strait of Georgia, plotted at 15 min intervals.

TABLE 4. Vertical distribution and horizontal travel of sockeye salmon No. 8516 during 9 h of its track, divided into five periods: (A) oriented movement ESE, (B) excursion into Howe Sound, (C) resumption of eastward movement, (D) continuation of eastward movement, and (E) circling off the mouth of Burrard Inlet. See Fig. 10 and 11 for details of the horizontal and vertical movements.

Depth interval	Periods of observation				
	(A) 11:36–13:35	(B) 13:36–15:30	(C) 15:31–17:30	(D) 17:31–19:00	(E) 19:01–20:30
1– 5 m	0.0 %	7.0 %	0.0 %	1.1 %	44.4 %
6–10 m	0.8	21.7	0.0	14.4	24.9
11–15 m	30.8	25.2	4.2	52.2	29.6
16–20 m	64.2	28.7	83.3	32.2	1.1
21–25 m	4.2	13.9	12.5	0.0	0.0
26–30 m	0.0	3.5	0.0	0.0	0.0
Mean	16.45	14.45	17.83	13.72	6.64
S. D.	1.95	6.30	2.03	3.41	4.62
Net km/h	3.48	1.40	3.70	3.74	1.50
Gross km/h	3.58	3.50	4.28	3.96	3.55
Net/Gross	0.97	0.40	0.86	0.94	0.42

Vertical movements of 8516, tracked in Georgia Strait near the Fraser River on August 22, 1985.

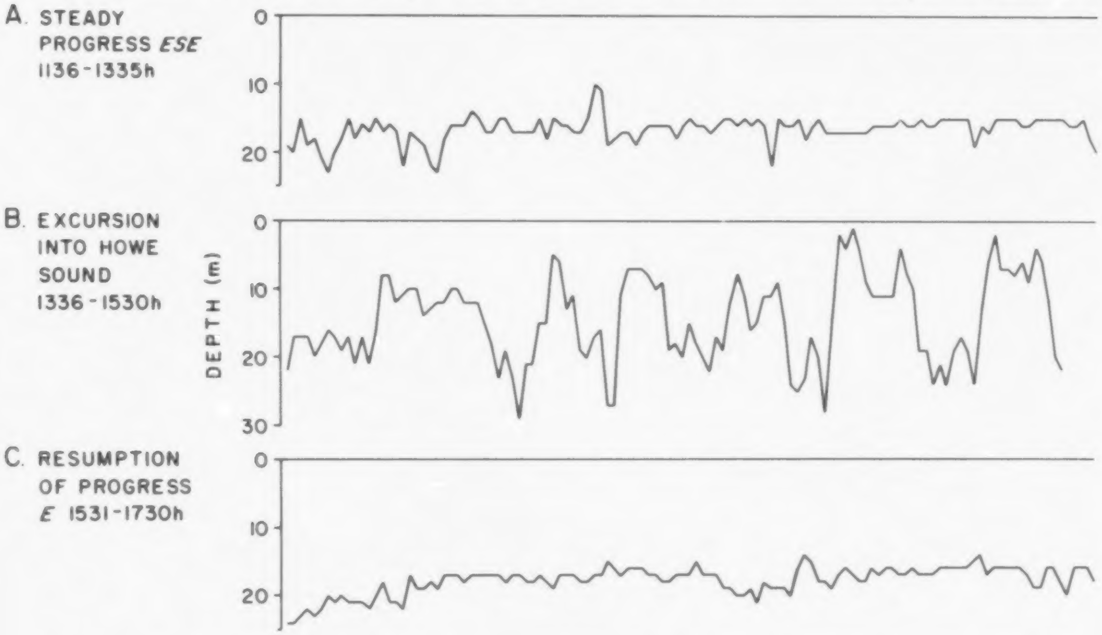


FIG. 12. Minute-by-minute record of the vertical movements of sockeye salmon No. 8516 during approximately 6 h of its track. Note increase in vertical movements during excursion into Howe Sound (see also Table 4).

oriented swimming (ratios of net/gross movement of 0.86 or greater) were also periods when the fish maintained a very narrow depth range (Table 4, Fig. 12). The excursion into Howe Sound and the circling off Burrard Inlet were characterized by more vertical excursions and lower net/gross movement ratios. Gross swimming speed, however, was only slightly slower during periods of circling.

The depth distribution of one fish, No. 8511, was bimodal (Fig. 10 A). This fish was released off the north end of Texada Island (Fig. 2) and swam WNW (net/gross ratio = 0.80) into and across a weakly ebbing tide. It continued WNW when the tide changed to a weak flood. The fish spent the first 120 min below 15 m and then began a sequence of 28 ascents (usually to 1-8 m) and descents (usually to 20-30 m) in the remaining 6 h of the track.

TAG RECOVERIES

Sixty sockeye were released with Petersen disc tags, including the 17 with transmitters. Of those, 5 with transmitters were recaptured by *Sea Luck* and 8 of the remaining 55 were returned by fishermen. These recoveries indicated variable patterns of horizontal movements. One fish released in northern Johnstone Strait moved 76 km towards the Fraser River in 2 days but another was caught 26 km farther from the river after 4 days. One fish released in northern Discovery Passage travelled 220 km to the Fraser and an additional 320 up the mainstem of the river to Lillooet in 12 days, for an average of 45 km/day. Two fish released in Deepwater Bay, just north of Seymour Narrows, were recovered 130 km south (no date) and 200 km south off the Fraser River in 5 days (40 km/day). Two fish released in the southern Strait of Georgia were recovered in the lower Fraser River after 6 days (56 km) and 2 days (30 km). Information on the last recovery was inadequate for an estimate of travel speed.

While the estimates of movement from the tag recoveries are highly variable, they imply a mean travel speed of 25 km/day (without accounting for direction of movement). This average is close to the 29 km/day average calculated for the salmon with transmitters by multiplying their net speed of 1.22 km/h × 24 h.

Discussion

Telemetry studies typically produce large amounts of data on small numbers of animals. Bearing this weakness in mind, the results of the present study permit certain generalizations about sockeye salmon movements and their relation to temperature and salinity. First, there appeared to be a general preference for near-surface waters. This was inferred from the shallow distribution of the fish in the vertically well-mixed waters in Discovery Passage. The waters in Johnstone Strait and Queen Charlotte Strait had regimes of changing temperature and salinity that generally extended from the surface to 20-30 m. As the fish in these waters spent virtually no time below 30 m, it may be stated that they occupied depths at or above the largest gradients. In the Strait of Georgia, however, the fish movements and the temperature and salinity patterns were more complex. The fish seldom descended into the cool (9-10°) saline (29-30‰) waters below 30 m. The fish also displayed no clear attraction to the warmest (16-18°) and least saline (27.5-23‰) surface waters. The magnitudes of the vertical excursions varied among the salmon, but most of the time was spent near the maximum gradients with major portions of time also spent above (Nos. 8511 and 8513) and below (No. 8512) this feature. These results agree with those of Ichihara and Nakamura (1982) who reported that chum salmon (*O. keta*) were surface-orientd and seldom descended below the thermocline.

The horizontal movements of the tracked salmon were more variable than their vertical movements. Some fish made substantial progress towards their presumed destination, the Fraser River, but others milled in back-eddies or swam into currents that would otherwise have aided their progress. Unfortunately, many of the tracks were of insufficient duration to properly characterize the movements of the individual fish. It is probably necessary to track a fish through at least one tide change to derive a meaningful picture of its movements. We had few recoveries of tagged salmon, but they clearly demonstrated the capacity for rapid homeward movement. These results agree with an early tagging study conducted in Deepwater Bay (Williamson 1927). He reported sockeye travelling from there to the Fraser River (176 km) in as little as 3 days, though most recoveries indicated much slower net movement. Disc tagging studies conducted in 1940 and 1941 indicated that the modal travel time from Johnstone Strait (Robson Bight) to the mouth of the Fraser River was 8 days (Verhoeven and Davidoff 1962). However, there was considerable variation, and the average time was 11.4 days for the 298 km distance, or 26.1 km/day. This average speed for net displacement is close to those of sockeye with transmitters and disc tags in the present study. These displacement rates are all lower than the 40–60 km/day estimates for maturing sockeye on the high seas (French et al. 1976).

In any tagging study, the longer the fish are at liberty, the smaller the effect of an initial handling delay will be. For this reason, interpretation of the horizontal movements of the salmon in the present study should be made cautiously. However, the vertical movements of individual fish became quite stereotyped after the initial dive and ascent, leading us to believe that our handling the fish may not have influenced their behavior unduly. The average ground speed observed in this study (2.39 km/h) agrees with the results of other sockeye ultrasonic tracking studies, including tracks of greater duration than ours (Madison et al. 1972; Stasko et al. 1976). This speed is similar to the optimal cruising speed of typical adult sockeye (Brett 1983), and seems to be typical for adults of this species. In general, it seems that differences in travel times among tagged fish are primarily related to directedness of travel and delay near the mouth of the river rather than differences in actual swimming speed.

The mechanisms guiding salmon in oceanic and coastal waters are the subject of considerable controversy. It has been proposed that salmon migrations from oceanic feeding grounds to the mouth of the natal river (where olfaction is presumed to guide them upstream) might be determined by kinetic responses to temperature and salinity (Leggett 1977; see also Neill 1979). Fish migrations were thus explained by the continuous optimization of the fish's external environment, as determined by seasonally changing physiological requirements. This hypothesis has been criticized by Groot and Quinn (1987), who pointed out that salmon migrations at sea occur over regions without regular, substantial horizontal changes in temperature or salinity. Our results indicate that movements in the water column can cause sockeye salmon to experience temperature changes of up to 8° in a matter of minutes, and they often swim in a constant direction through waters with no obvious horizontal gradients. Additionally, satellite observations revealed that the surface waters around Vancouver Island were a patchwork of warm and cool regions (C. Groot and A. Thomas, unpublished data). Nevertheless, the correlations between temperature and migratory route (Hamilton 1985) and timing (Burgner 1980; Blackbourn 1987) imply a direct or indirect relationship between some aspect of fish behavior and oceanographic conditions. Blackbourn (1987) has hypothesized that sockeye distributions are affected by water temperature during their last winter at sea: farther north when warm and farther south when cool. He attributed the correlations between temperature and migratory timing to the distribution of sockeye prior to homeward migration rather than to any influence during the migration itself.

It has also been proposed that the oceanic, coastal and riverine migrations of salmon are all guided by attraction to population-specific pheromones from emigrating conspecific juveniles (Nordeng 1977). Recent studies have indicated that Pacific salmon can indeed distinguish between populations based on odors (Quinn and Tolson 1986; Groot et al. 1986) and there was considerable spatial and temporal overlap between sockeye adult and smolt migrations in Johnstone Strait. However, the lack of coincidence between migratory routes of juvenile and adult sockeye salmon around Vancouver Island does not support the hypothesis that pheromones are the primary guidance mechanism (Groot et al. 1986).

Arnold and Cook (1984) reviewed the selective use of tidal flows as a mechanism facilitating fish migration in coastal waters. While the tidal currents were certainly fast enough for such a mechanism to operate, the fish did not behave accordingly. In Johnstone Strait the direction of tidal flow on the surface may be the reverse of that near the bottom, with negligible velocities at about 75–100 m, for a portion of most daily tidal cycles (Thomson 1981). Thus a salmon could theoretically descend to calm or even reversing currents when the ebbing tides generated westward currents on the surface. However, no evidence of tide-related vertical movements was evident in our tracking. Some bays and coves were present where the salmon could have found shelter from rapid adverse tidal currents. While they occasionally entered coves, this was not part of any consistent pattern of tide-related movement either.

Dodson and Dohse (1984) proposed a model of fish migration in coastal waters based on positive rheotactic responses to both ebb and flood tides and a pattern of reduced swimming speed and increased rate of turning to maintain position in the odor field of the river. Our sockeye salmon often swam into currents, but this was by no means a universal response. Passive drift was unusual, but the fish sometimes swam with relatively weak currents, especially in the Strait of Georgia. The waters between Vancouver Island and the mainland present difficulties for a migratory mechanism based on responses to currents because flooding tides aid travel towards the Fraser River in the northern region but hinder it in the southern region. Thus the characteristics of the water (oceanic vs. estuarine) brought in by the tides will be variable. Moreover, preliminary analysis of the current drogue data showed a very complicated current regime exhibiting large shears and directional variability, both vertically and horizontally. This was especially true in Discovery Passage, where current speeds were greatest. Finally, in assessing the model of Dodson and Dohse (1984), we must bear in mind that salmon do not always ascend their natal river as soon as they locate it. Groot et al. (1975) reported that sockeye in the Skeena River estuary often moved back and forth with the ebbing and flooding tides.

Smith et al. (1981) tracked Atlantic salmon (*Salmo salar*) and concluded that they tended to swim in geographic (compass) directions regardless of tidal current. This resulted in variable ground speeds and directions. Such a mechanism may operate, especially in waters with little influence from the home river. However, the present study produced equivocal evidence regarding this hypothesis. Some of our sockeye made direct movements that persisted through tidal changes but others such as No. 8509 displayed much more complex patterns. The excursion that No. 8516 made into Howe Sound (Fig. 11) was not consistent with compass orientation at that point in the migration. As the flooding tide moves north, Fraser River water is transported into Howe Sound and Burrard Inlet. When the tide ebbs, as it was doing when the fish entered Howe Sound, Fraser River water flows from these regions. It is perhaps not coincidental that the fish left the sound at 1530 h, when the tide turned to flood.

Westerberg (1982, 1984) and Døving et al. (1985) presented evidence that adult Atlantic salmon depth preferences are determined by gradients of temperature and salinity. Their salmon repeatedly swam through the steepest vertical gradients. Anosmic salmon made much greater vertical excursions and did not follow the thermocline (Døving et al. 1985). In this regard it is interesting that sockeye in the mixed region dove deeper than those in other areas. While the dives may have been an escape response, they may also have had an orientation function as the fish "sampled" the water column. Westerberg (1984) proposed that salmon use the current shear at gradients to indicate the source of the home odors. Our results generally support this hypothesis: little time was spent in the structureless deep waters below 30 m and vertical excursions were common. In the case of 8516, vertical excursions seemed to coincide with less directed horizontal movements. However, 8503 made both circuitous and direct movements while remaining very close to the surface, and 8514 moved in a rather direct manner across open water with many substantial vertical excursions.

A partial test of the hypothesis that sockeye are orienting to olfactory cues in the study area was provided by the pioneering experiment on olfaction and migration by Craigie (1926). Tagged sockeye released in Deepwater Bay (in a region of vertically mixed water) moved towards the Fraser River and several were caught upriver. Anosmic fish had a somewhat greater tendency to remain at the release site but almost all recoveries were in the direction of the Fraser River. Several were caught at the mouth of the river but only one was found any significant distance upriver. Craigie's results suggest that there may be a general southward preference which is gradually replaced by olfactory orientation as the fish find more distinct stratification. If the distinctive odors that characterize home streams are initially layered on the surface with the fresh water from the Fraser River, the tidally induced turbulence at Seymour Narrows almost certainly mixes them throughout the water column. It is known whether the odors subsequently concentrate on the surface along with the less dense fresher water. Olfactory orientation is probably a much simpler process in the Strait of Georgia than north of Seymour Narrows, though the mechanism of orientation to odors in open water without fixed reference points is still not obvious. The salmon did not prefer particular temperatures or salinities, nor did they prefer the warmest or least saline water. They were usually situated near the thermocline or near the surface in the absence of any gradients. These gradients are probably used for olfactory orientation, as they imply strong velocity shears. However, the rapid homing movements of some fish cannot be adequately explained by olfaction alone.

Acknowledgements

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The Regulation of Age at Maturity in Wood River Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

ROGERS, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*), p. 78–89. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The Wood River sockeye salmon commonly return from the sea in their fourth or fifth year and occasionally in their sixth year of life. An analysis of the age compositions of spawners and returning adults for 20 major spawning grounds in the lake system during 1952–84 revealed that freshwater age was most often determined by environmental factors (fish density and temperature) whereas ocean age was most often determined by the ocean age of the parents. Fish spawning in small shallow streams produce predominantly small 2-ocean fish, whereas those spawning in deep, fast-flowing rivers produce predominantly large 3-ocean fish.

Résumé

ROGERS, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*), p. 78–89. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les saumons nerkas de la rivière Wood effectuent généralement leur remontée au cours de leur quatrième ou de leur cinquième année et, parfois, au cours de leur sixième année. Une analyse de la composition des âges des géniteurs et des adultes en remontée vers 20 frayères importantes du bassin versant du lac, de 1952 à 1984, a montré que la durée passée en eau douce était généralement déterminée par des facteurs environnementaux (densité des poissons et température) tandis que la durée passée en mer était plutôt déterminée par la durée passée en mer des parents. Les poissons frayant dans de petits cours d'eau peu profonds produisent surtout de petits poissons passant deux ans en mer tandis que ceux frayant dans les cours d'eau profonds à débit rapide produisent surtout des poissons plus gros passant trois ans en mer.

Introduction

In 1946, the Fisheries Research Institute (FRI) began investigations of the abundance, distribution and age structure of the sockeye salmon (*Oncorhynchus nerka*) that returned to the spawning grounds of the Nushagak District in Bristol Bay. The studies were undertaken in response to declining catches in the fishery. The initial goal was to estimate the escapements to the lake systems and thus the annual runs (Gilbert 1968). In 1953, enumeration from streamside platforms or towers replaced aerial and ground surveys as the method of escapement estimation for the Wood River lake system and a few years later the escapements to the other large lake systems were also estimated by tower enumeration. However, the spawning surveys of Wood River lake system were continued because it was apparent, after a few years, that there were significant differences in the annual abundances and age compositions among the lakes and spawning grounds. It was felt that an explanation of this variation within the lake system would provide a better basis for management than provided by statistics based on the lake system as a whole; and perhaps provide some understanding of the long-term fluctuations in the abundances of runs (Rogers 1984a,b).

About 95% of Bristol Bay sockeye salmon mature after 2 or 3 years at sea after having spent 1 or 2 years in freshwater. Koo (1964) examined scales from Nushagak sockeye salmon that returned from the 1946–53 brood years. He observed that (1) fish that spent two years in freshwater tended to mature earlier, i.e., shorter marine life, than those that spent 1 yr in freshwater, (2) males were more likely to return after 2 yr at sea than females, (3) among sockeye of the same freshwater age, the amount and pattern of freshwater growth did not seem to affect their marine age at return, and (4) summer growth during the first year at sea (measured on scales from only males) did not seem to affect the marine age at return. Racial character (genetics) was believed to be one important factor responsible for age at return because some stocks contained predominantly 2-ocean fish, whereas others had predominantly 3-ocean fish.

Ricker (1972) pointed out that when genetic and environmental influences have been searched for adequately, both have been found. For each sockeye salmon stock or stock complex, it is not a question of whether there are genetic and environmental influences, but rather, the extent to which these influences operate and the extent that we can demonstrate these influences given the often imprecise statistics available.

Since Koo's work, we have accumulated 27 years of observations on the abundances and age compositions of parent spawners and theirs adult progeny in the Wood River lake system (returns from the 1953–79 brood years). In addition, we have observations on the growth of juveniles from the 1957 to 1983 brood years. I have analyzed these statistics (largely by correlation analysis) to determine the degree to which genetic and environmental influences have operated to regulate the age at maturity of Wood River sockeye salmon over this brief period in the history of the stocks.

Materials and Methods

LIFE HISTORY

The sockeye salmon in the Wood River lake system spawn primarily in August, September and early October (Marriott 1964). Time of spawning is rather precise for each stock. Fish that spawn in tributary creeks spawn earliest and those spawning along lake beaches spawn latest, whereas those spawning in the interconnecting rivers of the lake system are intermediate (last week of August–first week of September). For each type of spawning ground, the spawning is earliest in the lower or outlet lake and progressively later toward the upper or most interior lakes (Fig. 1).

The average air temperature usually drops below freezing by November and the lakes become ice-covered by December. Most sockeye salmon eggs hatch about March. The average air temperature usually rises above freezing in mid-April and thawing of winter snow and ice begins. Time of emergence is not known precisely (April–May?). Fry have been observed in abundance near creek mouths soon after the lakes were free of ice, which occurs about the first of June in the lower lake and about two weeks later in the uppermost lake. Near beach spawning areas in the upper lakes some just-buttoned-up fry have been observed as late as August, although they are not numerous.

The fry rear in the nearshore waters, where they feed on chironomids and littoral zooplankton, until late July–early August when they move offshore to the open waters of the lake (Rogers 1972). At that time they are about 4 cm long. They feed primarily on zooplankton and usually attain a length of 4–6 cm (1–2 g) by the first of September and about 7–8 cm (3–4 g) by late-October when water temperatures typically drop below 4°C. The fry are distributed in the surface waters at night and below 20 m during the day.

Nothing is known about their behavior or distribution during the winter. In the spring, most juveniles over 6.5 cm smoltify and seaward migration usually begins about the first of June or later if ice breakup is later. The Wood River smolts

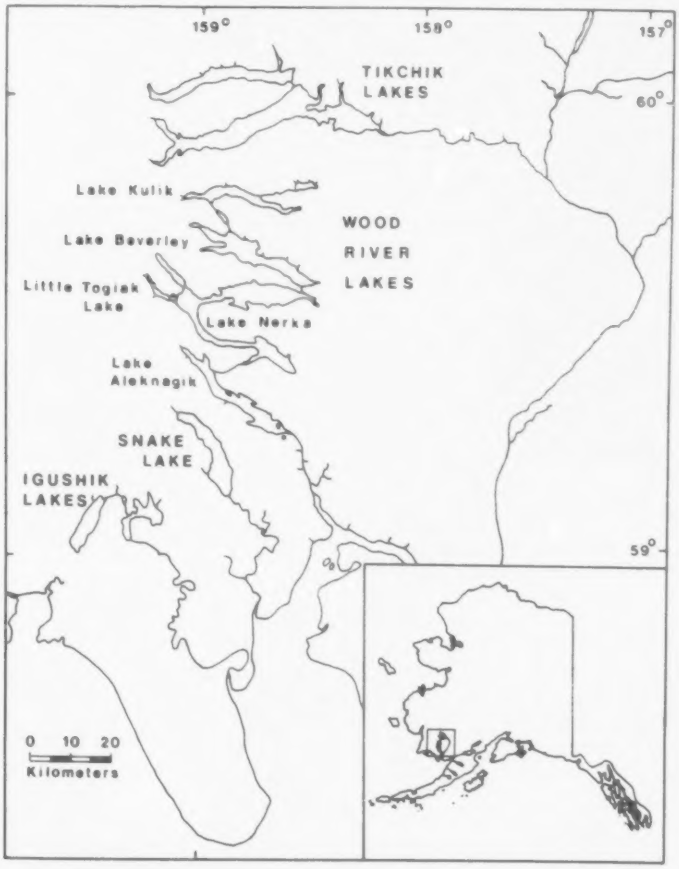

FIG. 1. Lakes of the Nushagak District of Bristol Bay.

are about the smallest in Bristol Bay and their seaward migration lasts the longest, extending into August (Eggers and Yuen 1984). Usually over 85% of the juveniles migrate to sea as yearlings weighing 3–5 g and the remainder migrate as 2-yr-olds weighing 8–9 g. Most other stocks in Bristol Bay migrate to sea in late-May or early June and the migrations often contain a majority of age 2 smolts.

The Wood River sockeye spend 2 or 3 years at sea. Jacks (1-ocean males) and 4-ocean fish are common, but in very low numbers. The majority return to Nushagak Bay and the lake system in the first 10 days of July. This short migration period is typical of most Bristol Bay stocks, but contrasts with the long period of seaward migration. The first adults usually arrive in the last week of June and the numbers of sockeye decline after mid-July with only a few thousand returning in late-July.

The specific distribution of Wood River sockeye salmon at sea is unknown, however, Nushagak sockeye salmon are distributed in the North Pacific from the eastern Gulf of Alaska to the western Aleutian Islands (French et al. 1976). During the winter, sockeye salmon are generally distributed south of the continental shelf and in the spring (April–May), when water temperatures are warming, the Bristol Bay sockeye move northward. The maturing fish arrive first and continue their homeward migration. The immature fish arrive on the shelf in late-June with the 2-ocean immatures somewhat earlier than the 1-ocean immatures.

About the first of July, south of Adak (1958–1978) immature sockeye salmon (predominantly Bristol Bay stocks) averaged 0.3 kg (age 1.1), 0.4 kg (age 2.1), 1.1 kg (age 1.2), and 1.2 kg for age 2.2 (Harris and Rogers 1979). In contrast, the age 1.2 and 2.2 mature fish that returned to Bristol Bay at about the same time, averaged 2.2 kg and 2.3 kg, respectively. The length frequencies of 2-ocean immature and mature sockeye salmon barely overlap at 50 cm (tip of snout to tail fork). The 3 ocean sockeye salmon in Bristol Bay averaged 3.1 kg with little difference between the freshwater ages. The annual average weights of sockeye salmon in Bristol Bay were correlated with the number of fish in the runs (Rogers 1980 and 1984a). Thus the average weight of Wood River sockeye salmon, especially age 1.3, is partly dependent on the abundance of other Bristol Bay stocks, particularly the most abundant Kvichak system stocks.

Within Bristol Bay, the Nushagak stocks are characterized by a high proportion of age 1. (fish that migrated to sea after 1 year) and within the Nushagak District, the Wood River stocks were characterized by a high proportion of age 1.2; however, the proportion of age 1.2 has decreased in

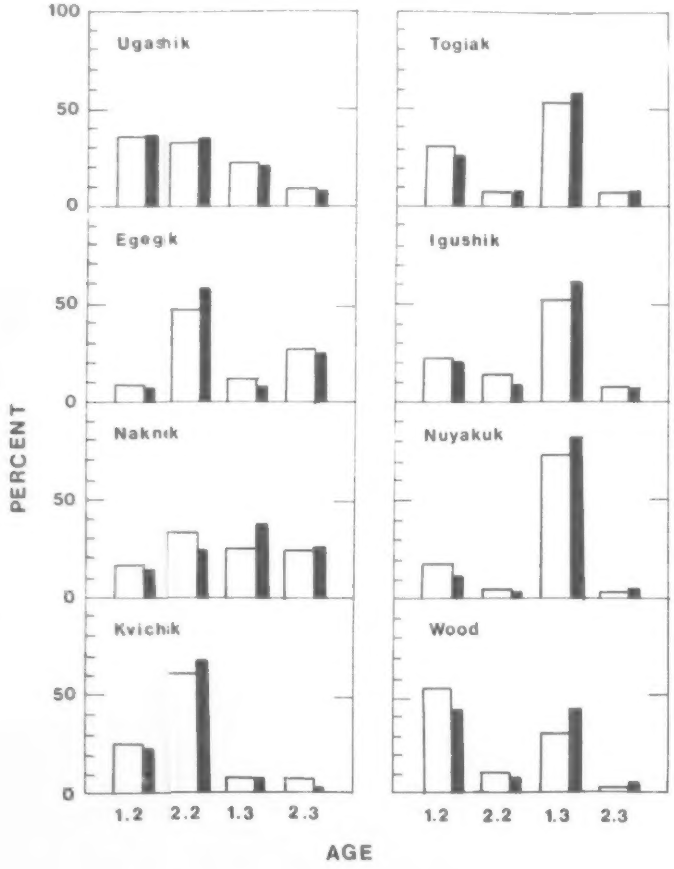

Fig. 2. Age compositions of the sockeye salmon that returned to the major Bristol Bay lake systems from brood years 1953–71 and 1972–79 (narrow bars).

TABLE 1. Average numbers of sockeye salmon (in thousands) and rates of exploitation in the Nushagak catches and escapements by age and sex; 1963–77 and 1978–83.

Years	Age 1.2		Age 2.2		Age 1.3		Age 2.3	
	M	F	M	F	M	F	M	F
1963–77								
Nushagak catch	143	100	43	38	178	264	21	27
Escapements:								
Wood River	181	249	30	39	140	168	14	14
Igushik	25	28	16	23	46	59	6	9
Nuyakuk	14	17	5	8	60	82	3	4
Exploitation (%)	36	23	44	35	42	45	53	53
1978–83								
Nushagak catch	722	652	156	139	1 394	1 577	142	146
Escapement::								
Wood River	387	548	57	82	282	330	26	27
Igushik	92	106	22	41	254	220	14	20
Nuyakuk	60	77	10	11	222	387	16	12
Exploitation (%)	61	48	65	51	62	63	61	62

recent years (Fig. 2). The abundances of all Bristol Bay stocks generally increased about 1978; however, only in the Wood River stocks was there also a significant change in age composition, i.e., from a predominance of 2-ocean fish to about equal proportions of 2 and 3-ocean fish. The cause of this change was sought in the abundances and ages in the individual spawning populations within the system.

THE FISHERIES

Prior to their return to Nushagak Bay, the Wood River stocks have been subjected to exploitation in the North Pacific by Japanese gill net fisheries (since 1955) and U.S. seine and gill net fisheries south of Unimak Island and in the Shumagin Islands (since the early 1900's). These fisheries certainly have the potential to alter the annual abundance and age composition in the Wood River runs and thus our estimates of the age compositions in the returns from each brood year. The Japanese fisheries exploited both mature and immature sockeye of age .2, thus those sockeye maturing at age .3 were subject to greater exploitation than those maturing at age .2. Unfortunately, precise estimates of the numbers of Wood River sockeye salmon caught by the interception fisheries are not available.

The Wood River sockeye salmon have been exploited in Nushagak Bay since the late 1800's. Prior to 1913, the stretched mesh size of the gill nets was 6–6$^1/_4$ inches. From 1913 to 1960, the mesh sizes were 5$^1/_2$–5$^3/_4$ inches and since 1961, the minimum mesh size permitted was 5$^3/_8$ inches. In the early fishery, the gill nets were probably very selective for 3-ocean fish compared to 2-ocean fish and for males compared to females (Mathisen 1971). During the 1950's, the fishery exploited 3-ocean females at twice the rate of 2-ocean females (Burgner 1964a).

The Wood River stocks are caught in the Nushagak fishery along with stocks bound for the other rivers draining into Nushagak Bay (Fig. 1). The Igushik and Nuyakuk (Tikchik Lakes) stocks were often abundant but usually were less abundant than the Wood River stocks (Table 1). The Nushagak–Mulchatna Rivers also contributed an average of

TABLE 2. Average lengths (mid-eye to tail fork, mm) and weights (kg) of sockeye salmon in the Nushagak catches and escapements by age and sex; 1963–77 and 1978–83.

Years	Age 1.2				Age 1.3			
	Male		Female		Male		Female	
	L	W	L	W	L	W	L	W
1963–77								
Nushagak catch	523	2.45	510	2.14	589	3.57	562	2.90
Escapements:								
Wood River	513	2.3[a]	492	1.9	577	3.4	551	2.8
Igushik	528	2.6	501	2.1	591	3.8	556	2.9
Nuyakuk	503	2.2	494	1.9	592	3.9	553	2.9
1978–83								
Nushagak catch	520	2.40	504	2.07	584	3.46	555	2.81
Escapements:								
Wood River	513	2.3	487	1.8	579	3.5	552	2.8
Igushik	532	2.6	508	2.2	594	3.9	562	3.0
Nuyakuk	511	2.3	500	2.0	595	4.0	562	3.0

[a] Fish were weighed in samples from escapements in only a few years, in most years mean weight was estimated from mean length and a weight–length regression.

60 000 sockeye to the district escapements during 1963–77 and an average of 140 000 in recent years (1978–83). The Snake River received averages of 12 000 and 15 000 for the two periods. The escapements to the two minor systems were usually estimated by aerial surveys, and sample sizes to determine age, length and sex were usually small.

About 2 000–3 000 fish were sampled annually from the commercial catch beginning in 1946, and 1 000–2 000 fish were sampled by seining in each major river to determine the age-sex compositions and average body size in the escapements beginning in 1959. Spawning ground samples were used to determine the compositions of escapements during 1946–58. FRI conducted the sampling prior to 1960 and the Alaska Department of Fish and Game (ADF&G) has done so since 1961 (Burgner 1964b; Yuen 1984).

The annual catch by age–sex group was apportioned to each river system according to the numbers in each age–sex group in the escapements to estimate the runs.

Thus it was assumed that for each age–sex group, the fish bound for the different rivers were equally vulnerable to the fishery. However, there were some significant differences in the average size of the sockeye in the escapements (Table 2). The 3-ocean fish in the Igushik and Nuyakuk escapements were generally larger than those in the Wood River escapements and the 2-ocean fish in the Igushik escapements were usually larger than those in the other escapements. The possible bias in apportioning the catches is probably not as great as indicated by the differences in sizes of sockeye, because in most years the majority of the escapements have come during closed periods in the fishery. This has been especially so in recent years as the efficiency of the fleet has increased to the point that it can catch over 80% of the fish in Nushagak Bay in about 24 h (note the change in the differences in exploitation among age–sex groups in Table 1).

THE SPAWNING GROUNDS

Sockeye salmon spawn in the Wood River lake system along lake beaches where there is upwelling groundwater, in the interconnecting rivers between the large lakes (primarily between Lake Beverley and Nerka and between Lake Nerka and Aleknagik), and in many spring or small lake-fed streams. There are also several runoff streams (from rain or snow) in the system, but these seldom contain spawning salmon as they are very unstable and many are dry or frozen solid in winter. There are about 62 major spawning grounds (i.e., ones that typically contain over 1 000 spawners) within the lake system.

Of the 24 spawning grounds for which we had annual age compositions, I calculated the age compositions of the returns for 12 areas. These were chosen on the basis of the completeness of the data set and the relative precision of the abundance estimates. Linear correlation coefficients were calculated for the freshwater age compositions (percent age 2.) and ocean age compositions (percent age .3) for adult returns and male parents, female parents and combined sexes. The data were also plotted and visually examined for nonlinearity.

The spawning surveys are scheduled according to the average time of spawning in the lakes. The aerial surveys are used to estimate the numbers of spawners along beaches, in the rivers and in larger creeks, whereas ground surveys are used to count the numbers spawning in smaller creeks (less than 6 km in length). ADF&G has conducted the aerial surveys since 1960 (e.g., Nelson 1979), and FRI has conducted the ground surveys and collected samples to determine the age composition (usually 100 males and 100 females from each of 24 spawning grounds). Age was determined from scales and lengths (ocean age) until 1960 when we began collecting otoliths to determine age. Otoliths were determined to be more accurate and were easier than scales to collect on the spawning grounds (Kim and Roberson 1968).

The age compositions of males and females were averaged according to the estimated sex ratio in the escapement to the lake system because reliable estimates of sex ratio could not be obtained on the spawning grounds. The escapement by age-group in each sampled spawning ground was then expanded by the ratio of run (catch and escapement) to escapement in the lake system to estimate the run by age to the spawning ground. The runs by age-group were then arranged according to brood year and the age composition of the return was calculated.

The greatest source of error in the age composition of the adult returns (from a brood year) was in the annual estimates of the numbers of fish on the spawning ground. There appeared to be little difference in the run timing to various spawning grounds (Rowse 1985). Repeated sampling indicated that the age compositions of the spawners were fairly precise, i.e., within one or two percentage points; however, mark–recapture studies and some tower enumeration within the lake system indicated that spawner estimates for the rivers and lake beaches were only within about ± 60% of the actual number (Roberson 1967 and 1968; Rogers 1984b). The ground counts for the smaller creeks were much better, but contained a bias of about 15% because some fish that entered a stream were carried off by bears or buried in the gravel, although most bear kills were counted because they usually do not eat the fish's head.

Considering all the possible sources of error from interannual variation in the exploitation by foreign and domestic fisheries to the estimates of spawner abundance, we should not expect a very close correlation between age compositions of spawners and returning adults even if the true correlation were near unity, i.e., age at maturity was entirely determined by the age of the parents.

Results and Conclusions

The Nushagak stocks were the first stocks in Bristol Bay to be extensively exploited by a commercial fishery. After the development of the fishery in the 1800's, there followed a period of about 20 years with relatively stable production with an average annual catch of 5 million sockeye. A decline occurred about 1919 and this was followed by a 30-yr period in which the catches averaged about 3 million (scale samples from the catches are available for most of this period). Another decline occurred about 1949 and the annual catches averaged about 1 million until 1978 when salmon abundance generally increased throughout western Alaska (Fig. 3). Mathisen (1972) reconstructed the Nushagak escapements in the early periods and concluded that the selectivity of the fishery for 3-ocean fish was only a contributing factor in the declines in the catches but not the primary cause, which was

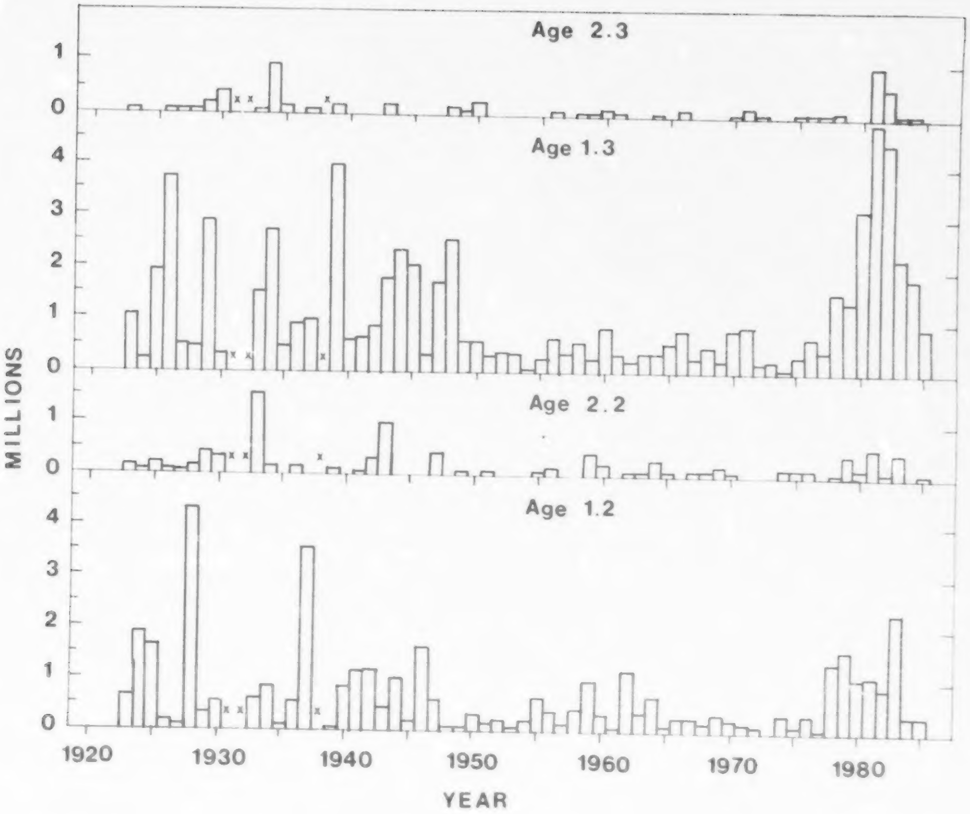

FIG. 3. Annual catches of sockeye salmon in the Nushagak District by major age group, 1923–85.

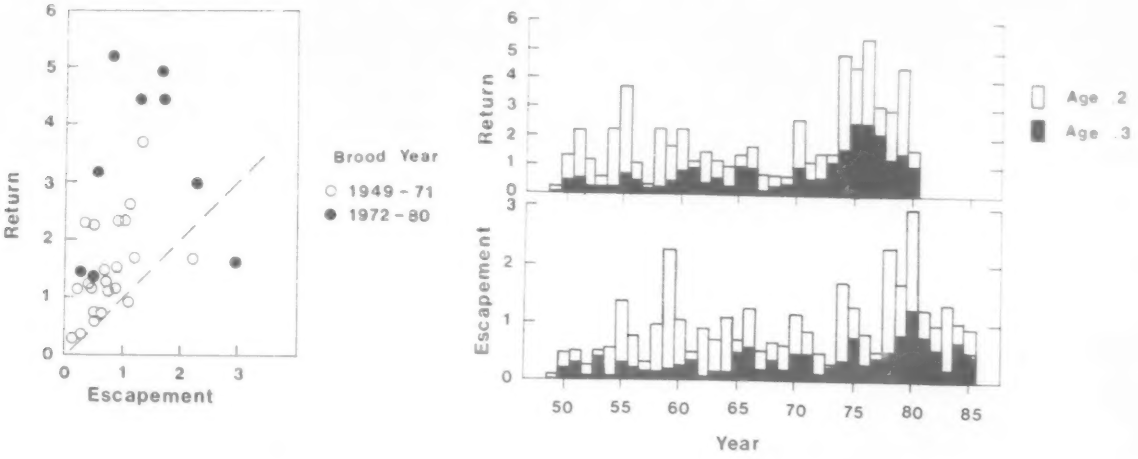

FIG. 4. Escapements and returns of sockeye salmon to the Wood River lake system, 1949–85.

TABLE 3. Escapements to the Wood River lake system, subsequent mean weights of fry (on 1 September) and smolts, and age composition and adult returns from the 1953–82 brood years.

Brood	Escapement		Mean weight (g)			Adult return		
year (y)	Number (10^4)	% .3	Age 0 (y+1)	Age 1 (y+2)	Age 2 (y+3)	Number (10^4)	% .3	% 2.
53	52	75	—	4.7	6.9	63	58	15
54	57	9	—	4.2	6.1	227	14	37
55	138	20	—	3.5	8.4	368	20	18
56	77	28	—	4.4	9.1	106	41	2
57	29	56	2.1	5.6	11.3	38	62	11
58	96	14	2.0	5.8	7.7	234	14	5
59	221	8	1.4	4.3	7.9	164	25	25
60	102	23	1.7	4.2	9.3	228	36	8
61	46	79	1.7	5.1	8.5	117	76	4
62	87	6	1.8	4.8	9.9	152	26	9
63	72	20	1.4	5.6	7.5	124	51	7
64	108	13	1.4	4.3	6.2	97	32	37
65	68	69	1.2	4.5	—	145	63	15
66	121	48	1.6	—	—	164	45	5
67	52	31	2.4	—	—	76	21	14
68	65	54	2.1	—	—	73	47	3
69	60	25	2.0	—	—	74	66	38
70	116	40	1.7	—	—	260	35	9
71	85	53	1.5	—	—	116	46	18
72	43	23	2.0	—	10.1	134	45	5
73	33	87	2.3	5.1	6.5	142	82	7
74	171	20	1.3	4.4	9.3	493	33	9
75	127	60	1.1	3.4	5.8	443	56	23
76	82	32	1.3	4.1	9.4	518	48	15
77	56	66	2.1	7.0	7.0	316	67	2
78	227	23	1.4	3.7	8.4	296	42	23
79	171	46	1.0	5.5	8.3	441	36	1
80[a]	297	41	1.6	4.4	8.0	(160)	(65)	(12)
81	123	63	1.5	6.5	9.0	—	—	—
82	98	56	2.2	7.6	—	—	—	—

[a] Returns based on preliminary data from the Alaska Dept. Fish and Game and an estimate of age 2.3 returns in 1986.

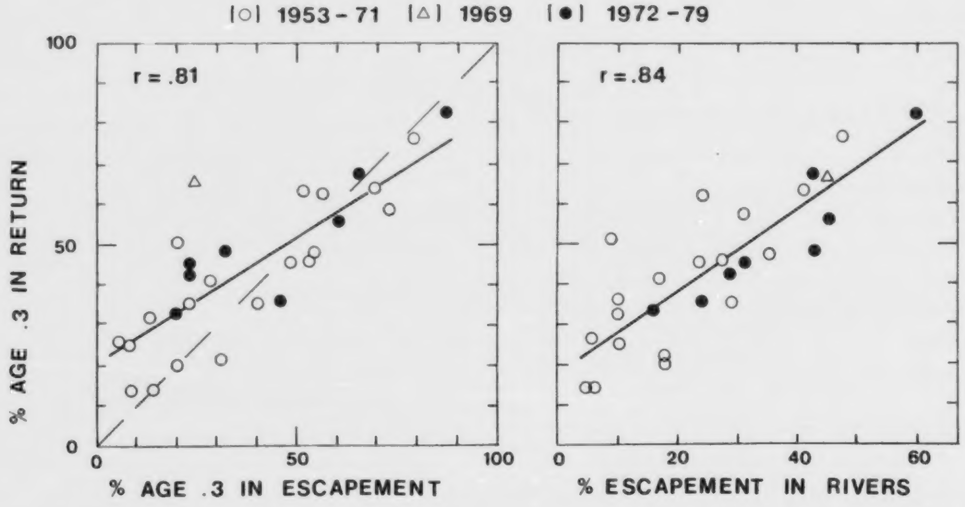

FIG. 5. Correlations between the ocean age compositions of sockeye salmon returns to Wood River and the ocean age compositions of parent escapements (*left*) and the percentages of the escapements that spawned in two rivers within the lake system (*right*).

TABLE 4. Average number and relative variation (COV) in spawners and adult returns to selected spawning grounds in the Wood River lake system and the ocean and freshwater age compositions, 1953–79 brood years.

Lake		Spawners					Adult returns				
		Number (10³)		Age composition			Number (10³)		Age composition		r[c]
Location	Type[a]	Mean	COV	% .3	% 2.	n[b]	Mean	COV	% .3	% 2.	(% .3)
Aleknagik											
Hansen	SC	4	95	30	18	27	6	97	29	21	.53
Happy	MC	2	68	49	22	23	—	—	—	—	—
Bear	MC	4	58	41	12	27	8	76	51	16	.77
Ice	LC	7	59	67	11	21	—	—	—	—	—
Agulowok	LR	130	71	77	10	27	357	97	85	14	.34
Nerka (South arm)											
Fenno	MC	3	107	30	4	27	5	122	36	5	.85
Stovall	MC	8	174	23	5	23	—	—	—	—	—
Lynx	MC	2	113	19	5	25	6	120	25	9	.61
N4-N6	B	8	52	32	8	25	—	—	—	—	—
Pick	MC	12	121	30	4	27	23	101	36	5	.77
Little Togiak	SR	7	69	38	6	25	17	80	47	9	.53
Nerka (North arm)											
Hidden	SC	3	126	20	4	21	5	114	24	3	.84
Anvil Bay	B	19	74	30	7	27	—	—	—	—	—
Kema	MC	5	114	23	7	24	—	—	—	—	—
Agulukpak	LR	93	71	66	8	27	307	97	77	12	.61
Little Togiak											
"C"	SC	0.4	112	16	14	17	—	—	—	—	—
Beaches	B	23	56	38	16	27	56	85	44	20	.78
Berveley											
Moose	MC	4	95	22	6	20	—	—	—	—	—
Hardluck Bay	B	12	118	15	12	24	—	—	—	—	—
B9-B12	B	8	114	12	17	17	—	—	—	—	—
Silver Horn	B	28	92	18	13	19	—	—	—	—	—
Mikchalk	B	16	91	17	14	17	—	—	—	—	—
Kulik											
Beaches	B	80	110	14	19	23	170	114	16	20	.48
Grant	SR	10	88	20	14	27	21	79	23	15	.47

[a] SC = small creek; MC = medium size creek; LC = large creek; LR = large river between lakes; SR = small river between lakes; B = lake beach.

[b] Number of years with scale or otolith samples for age composition.

[c] Linear correlation coefficient between % .3 in spawners and % .3 in adult returns (excluding the 1969 brood year).

a reduction in the return per spawner. However, if age at maturity was largely inherited and an important factor in the reproduction of some spawning populations, then the selectivity of the fishery may have been a major factor in at least the early declines in the fishery.

The Wood River stocks contained a predominance of 2-ocean fish in the escapements and returns during the 1950's and 1960's (Fig. 4, Table 3). The proportions of 3-ocean fish increased somewhat in the 1970's and following two very small runs in 1972 and 1973, the Nushagak fishery was greatly restricted in 1974 and 1975. This allowed relatively larger numbers of 3-ocean than 2-ocean fish to enter the spawning grounds. Therefore, when conditions for ocean survival improved (reduced high seas fishing and warmer temperatures) there were proportionately greater increases in the returns of 3-ocean fish than 2-ocean fish (Rogers 1984a).

Since 1953, when tower enumeration began, there has been no correlation between freshwater age in parent escapements and freshwater age of adult returns; however, there has been a significant correlation between the ocean age composition in escapements to the Wood River system and the ocean age composition of the adult returns (Fig. 5). There was an especially close correlation when the percentage of 3-ocean fish in the escapement was over 40%. At lower percentages, the correlation was rather weak and there was a tendency for a higher percentage of 3-ocean fish in the returns than in the escapements.

There was one particulary deviant observation concerning 1969 brood year fish where the percentage of 3-ocean fish in the returns was much higher than expected from the percentage in parent spawners. The spring and summer of 1971 (when the age 1 smolts from 1969 spawning migrated to sea) was the coldest on record for western Alaska. The age 1.1 sockeye salmon sampled at Adak in early July, 1972 were also the smallest observed during 1958–1978 (Harris and Rogers 1979). The temperatures at sea were also much colder than average in 1972 (Rogers 1984a). It seems apparent that the fish from the 1969 brood, which had experienced good freshwater growth in 1970 (Table 3), were partly inhibited from migrating in 1971 by the exceptionally cold weather and that those that did migrate experienced unusually poor growth at sea which delayed their age at maturity.

Excluding the 1969 brood year, the ocean age composition of the Wood River escapements explains about 72% of the variation in the ocean age composition of the adult

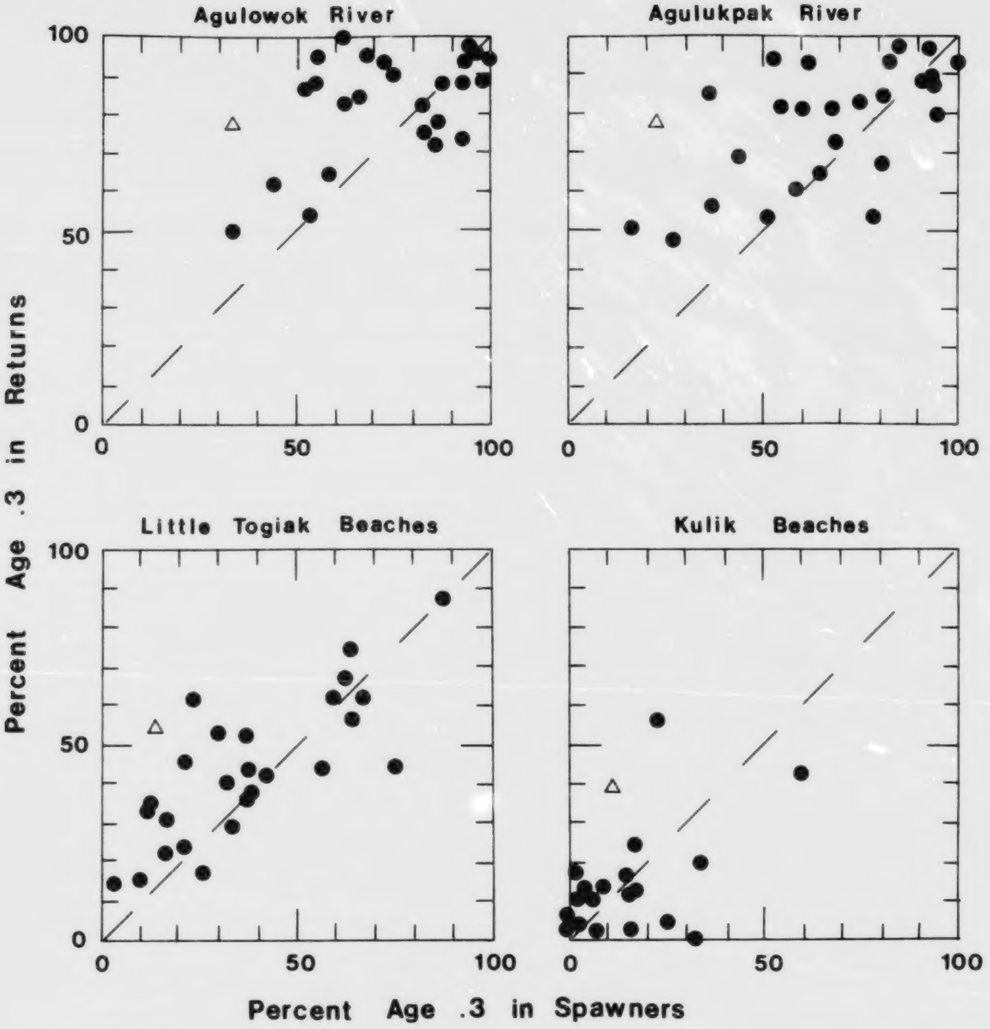

FIG. 6. Plots of the ocean age compositions of returns on the ocean age compositions of parent spawners for two rivers and two lake beach spawning areas, 1953–79 brood years (triangles are for the 1969 brood year).

returns; however, nearly the same amount of variation was explained by the percentages of the escapements that spawned in the two largest interconnecting rivers in the system (Algulowok and Agulukpak) because they usually contained the majority of 3-ocean fish in the escapement. Thus, statistics from mixed stocks can be misleading. To determine the extent that age at maturity may be inherited, we must examine relationships between parents and progeny on the spawning grounds.

The statistics on spawners and adult returns to the spawning grounds in the Wood River lake system are presented in Table 4. There were no significant correlations for freshwater age and no significant difference in the correlations of ocean age of spawners and adult returns between male and female spawners. The age compositions of the sexes were very similar, except for the river spawners, where there were higher percentages of 3-ocean fish in females than in males. The correlations between ocean age composition of spawners and adult returns were generally lower ($r = 0.34$–0.85 excluding 1969) than the correlation for the lake system. However, the degree of correlation was nearly as high for those spawning grounds where we had the best estimates of spawner abundance, i.e., small and medium size creeks and Little Togiak Lake.

An unanticipated result of the analysis was the correlation between the relative variation (coefficient of variation) in numbers of spawners and in returns and the percentages of 3-ocean fish. Spawning populations with low percentages of 3-ocean fish were more variable in numbers than those with a more even age composition. In addition, populations with higher percentages of age 2. fish (2 yr rather than 1 yr in freshwater) tended to be less variable in numbers of spawners and returns than populations with very low percentages of age 2. This indicates that populations with a variable age at maturity are more stable numerically than those with predominantly one age, and suggests that age-selective fisheries would induce interannual variability in these populations and thus variability in the catches and runs to the lake system.

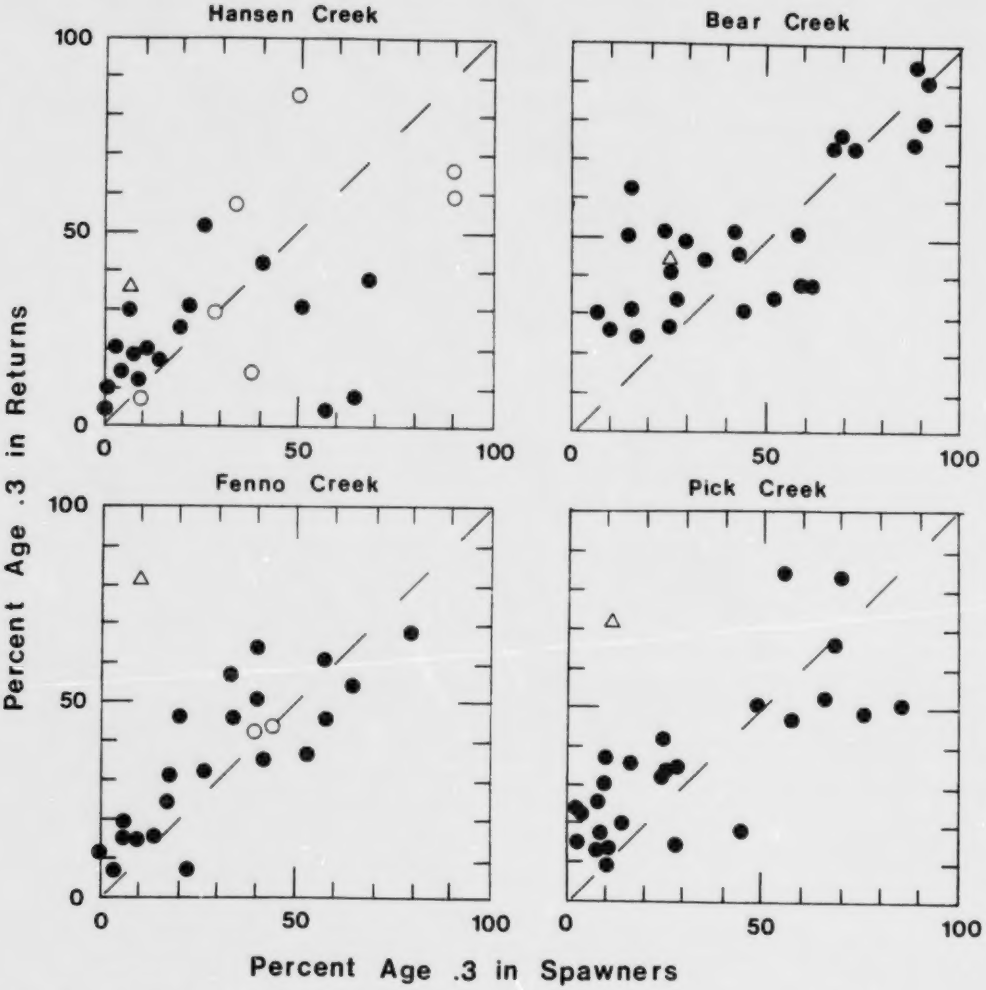

FIG. 7. Plots of the ocean age compositions of returns on the ocean age compositions of parent spawners for two creeks in Lake Aleknagik (*top*) and two in Lake Nerka (*bottom*). Open circles are for years with small returns (1 000 or less) and the triangles are for the 1969 brood year.

Examples of the correlations in ocean age compositions for the individual spawning grounds are shown in Fig. 6 and 7. The Lake Kulik beach spawners are typical of the other beach spawners in the upper lakes of the system (those in Lakes Mikchalk and Beverley). During 1953–79, there were few years in which more than 20% of the spawners were 3-ocean fish and in those few years, spawners were few in number. It would seem that if these beach spawning areas received some large espacements with a majority of 3-ocean fish, they would produce more 3-ocean fish in the returns. At least there is no obvious reason why 3-ocean fish should be at any disadvantage in beach spawning areas. On the other hand, 3-ocean fish would seem to have an advantage in reproduction in the two large interconnecting rivers, where the substrate is rather compact and water velocity and depth are usually greater than in the creeks and small rivers. However, even in years when 2-ocean spawners were in the majority, there was a majority of 3-ocean fish in the returns.

The small streams (less than 2 km long, less than 5 m wide and an average depth of less than 20 cm) tend to have lower percentages of 3-ocean fish than most medium-sized streams, and the largest stream surveyed, Ice Creek; (11 km long, 16 m wide and an average depth of 35 cm) has the highest percentage of 3-ocean fish. Hansen Creek has an average depth of about 9 cm. Excluding years when the returns were low (and the precision of the age composition estimates was poor) it appeared that 3-ocean fish, when in the majority, were not as productive as 2-ocean fish because the numbers of 3-ocean fish in the returns actually declined. In this very shallow stream, 3-ocean males would have a special difficulty in swimming and avoiding predators, primarily the Alaska brown bear and the glaucous-winged gull.

These results indicate that ocean age of the Wood River stocks is largely inherited (probably through regulation of growth rate or behavior) and that the spawning environment may alter age at maturity through differential reproductive success of small and large individuals. An unusually cold year apparently caused the Wood River stocks to mature later, but several recent warm years did not significantly affect age at maturity except indirectly. The Wood River

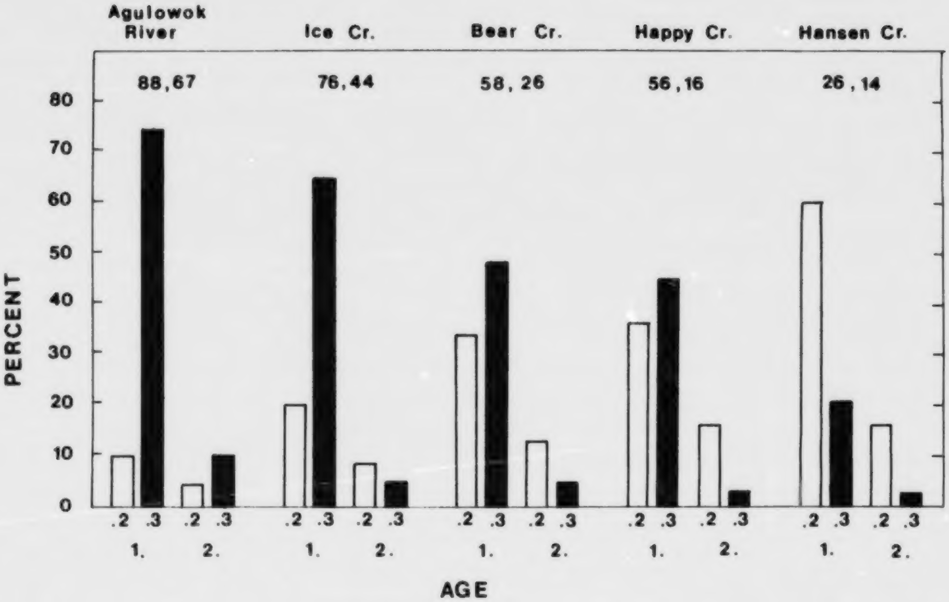

FIG. 8. Age compositions of the sockeye salmon returns to five spawning grounds in Lake Aleknagik from the 1953–79 brood years. The percentage of age .3 fish in the returns by freshwater age are given for each stock.

sockeye tend to migrate to sea after one summer's growth, but when fish density in the lake was high or temperature very cold, some proportion of the juveniles (rarely over 50%) held over for an additional year. Those fish then tended to mature earlier at sea (probably because of the large size at seaward migration, Table 3).

Within a lake, the alteration of ocean age at maturity from an additional year in freshwater varied by population according to the ocean age of the parents (Fig. 8). For the Agulowok River population, 88% returned as 3-ocean fish from those that had spent 1 yr in the lake whereas 67% returned as 3-ocean fish from those that had spent 2 yr (still the majority). The shift in ocean age with the change in freshwater age was greater in the populations with relatively even ocean age distributions, than those with predominantly 3-ocean or 2-ocean spawners (Agulowok River and Hansen Creek).

Future research on the Wood River spawning populations is recommended, with focus on the variability in body size among spawning populations by studies similar to those by Beacham and Murray (1985) on pink and chum salmon. This is needed to examine the assumption of equal exploitation rates (by age or sex) on the populations. In addition, we need more detailed measurements on the physical parameters of the spawning grounds to help explain observed variation in ocean age and a study of bear predation on sockeye salmon spawners with special emphasis on possible selectivity for age and sex.

Acknowledgments

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Maternal Size Effects May Explain Positive Correlations Between Age at Maturity of Parent and Offspring Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

Bradford, M. J., and R. M. Peterman. 1987. Maternal size effects may explain positive correlations between age at maturity of parent and offspring sockeye salmon (*Oncorhynchus nerka*), p. 90–100. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Bristol Bay, Alaska sockeye salmon (*Oncorhynchus nerka*) stocks tend to show a positive correlation between parents and offspring in the duration of oceanic life (ocean age). Although this might be interpreted as evidence of genetic inheritance, we tested an alternative hypothesis, which was a modification of Bilton's maternal effects mechanism. Analysis of mean age data from nine Bristol Bay sockeye stocks shows that in four stocks, our hypothesis appears to be at least as likely an explanation of the positive correlation in ocean ages as the genetic hypothesis. In those cases, in years when female spawners were larger (older ocean age), their offspring smolted at an early age, presumably because of the documented size advantage imparted by large females on their offspring through larger egg and fry size. However, fish which smolted at an early age spent longer in the ocean before maturing. These relations created a positive correlation between ocean ages of parents and their offspring without implying direct genetic inheritance of age at maturity. Our mechanism only applies to stocks where more than one smolt age is common; it does not explain the offspring-parent age correlation seen in Babine Lake sockeye, for example.

Resumé

Bradford, M. J., and R. M. Peterman. 1987. Maternal size effects may explain positive correlations between age at maturity of parent and offspring sockeye salmon (*Oncorhynchus nerka*), p. 90–100. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Il semble exister une corrélation positive entre les périodes passées en mer des parents et de la progéniture chez les stocks de saumon nerka (*Oncorhynchus nerka*) de la baie Bristol (Alaska). Ce phénomène peut être interprété comme un trait génétique, mais nous avons testé une autre hypothèse, à savoir une modification du mécanisme des effets maternels de Bilton. L'analyse des données sur l'âge moyen de neuf stocks de saumon nerka de la baie Bristol a montré que pour 4 stocks notre hypothèse était aussi valable que l'hypothèse génétique pour expliquer la corrélation positive entre les périodes passées en mer. Ainsi les années où les géniteurs femelles étaient plus gros (temps plus long passé en mer), la progéniture atteignait le stade de smolt plus tôt; sans doute à cause de l'avantage de taille conféré par les grosses femelles produisant des oeufs et des alevins plus gros. Les poissons qui atteignent plus tôt le stade de smolt restent cependant plus longtemps en mer avant de devenir matures. Ces relations créent une corrélation positive entre le temps passé en mer des parents et de leur progéniture, ceci sans qu'il soit nécessaire de supposer la transmission génétique directe d'un caractère lié à l'âge à la maturité. Notre mécanisme ne s'applique cependant qu'aux stocks où il est courant que les smolts ne soient pas du même âge; il ne peut expliquer la corrélation entre l'âge de la progéniture et des parents notée, par exemple, chez le saumon nerka du lac Babine.

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Introduction

Sockeye salmon (*Oncorhynchus nerka*) show considerable variation in age at maturity (Foerster 1968). This age depends on the duration of freshwater life (usually 1 or 2 years before reaching the smolt stage) and on the duration of ocean life (usually 2, 3 or 4 years). It is important to understand the causes of variation in age at maturity because the weight of fish at the time they become vulnerable to fishing gear is correlated with the duration of their ocean life (ocean age) (see Rogers 1980, his fig. 11–12 and Ricker 1982). Over 99% of adult weight is gained in the ocean.

Some stocks of sockeye salmon in Alaska and British Columbia show a positive correlation between mean ocean age of parent spawners and mean ocean age at maturity of their offspring (Larkin and MacDonald 1968; Rogers 1984; Peterman 1985). This tendency for the age at maturity of fish to be correlated with that of their parents could be caused by some genetic mechanism of inheritance. If this were true, then the correlation between size and ocean age, along with size-selective fishing by gillnets, could tend to cause a directional change in age at maturity over time (Ricker 1981). However, before drawing such a conclusion, we should evaluate other mechanisms which affect age at maturity and which might also lead to the observed pattern of parent–offspring correlations.

There are currently three known processes which affect the between-year variation in age at maturity of sockeye salmon. First, Godfrey (1958) and Ricker (1972) provide some support for inheritance of age at maturity. Second, age at maturity is known to be affected by environmental conditions which influence a brood's freshwater growth (Hyatt and Stockner 1985; Rogers 1980; Peterman 1982), as well as its saltwater growth (Bilton 1970; Krogius 1960). Third, Bilton (1970, 1971) proposed that the size of female spawners could affect age at maturity of their offspring simply through the known positive correlations between female size and size of her eggs, and between egg size and fry size, and the effect of fry size on subsequent life stages.

In this paper, we explore a fourth, new process which may affect age at maturity. This mechanism is an extension of Bilton's maternal effects hypothesis to stocks for which smolt age can vary. Our hypothesis can lead to a positive correlation between ocean age of parents and that of their offspring, but does not assume direct genetic inheritance of ocean age.

Details of the various mechanisms which may affect age at maturity are given below.

GENETIC INHERITANCE MECHANISM

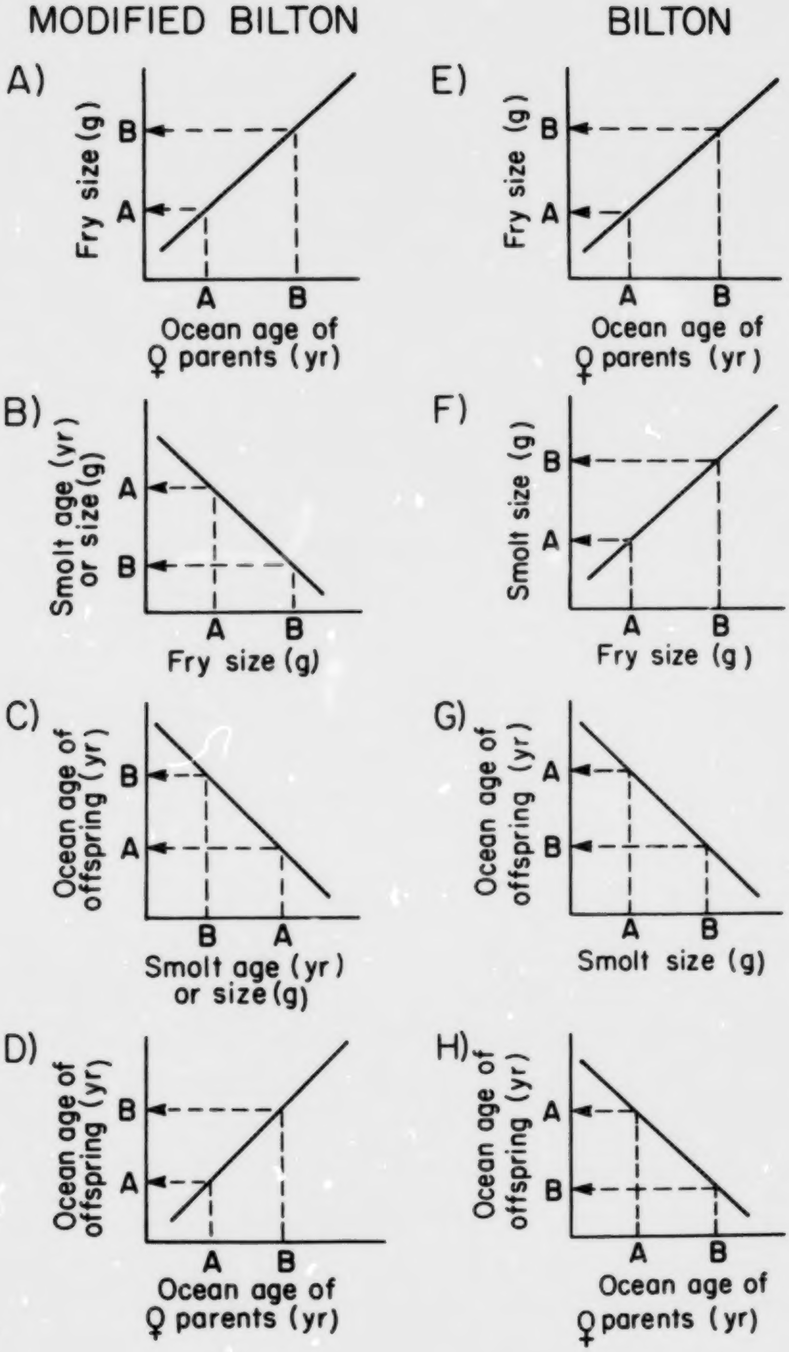
This mechanism assumes inheritance of ocean age at maturity directly, most likely implying a large component of additive genetic variance (Falconer 1960), and possibly including dominance and interactive effects. While some evidence for this mechanism has been reported for other salmonids (Ricker 1972; Gardner 1976; Thorpe et al. 1983), evidence for sockeye salmon is relatively weak (Ricker 1972), and it is not based on controlled breeding experiments (e.g. Godfrey 1958; Rogers 1987). If variation in ocean age at maturity of sockeye is mostly due to genetic inheritance, then there should be a positive correlation between ocean age of parents and that of their offspring.

ENVIRONMENTAL MECHANISM

Under a certain set of conditions, environmental influences on ocean age at maturity can also generate the observed positive correlation in offspring and parental ocean ages. Freshwater environmental factors such as fish density, temperature, and lake productivity can affect freshwater growth of sockeye (Rogers 1973, 1980; Brocksen et al. 1973; Hyatt and Stockner 1985). The resulting freshwater growth determines size at smolting, and in many stocks that size is inversely correlated with ocean age at maturity (Hyatt and Stockner 1985; Peterman 1982; Bilton 1971). Backcalculations of ocean growth from adult scales also shows that rapid ocean growth tends to lead to earlier ocean age at maturity (Krogius 1960; IPSFC 1962; Bilton 1970). If environmental conditions are a major determinant of variation in ocean age at maturity, and if those conditions vary randomly in time, then there should be no correlation between ocean age of offspring and that of their parents. At the very least, such variation should tend to obscure the correlation resulting from some other mechanism. However, a long-term directional time trend in environmental conditions could give rise to a positive correlation in ocean ages. For example, a continuing improvement in ocean conditions for sockeye growth over a long period could cause parents to mature earlier than normal, as well as their offspring, creating the observed positive correlation in ocean ages (Peterman 1985). If this latter situation existed, we would expect to see, (1) a time trend within the correlation plots, and (2) a long-term time trend in some freshwater or saltwater environmental variable.

MATERNAL EFFECTS

Bilton's (1970, 1971) maternal effects hypothesis provides another means by which parental age affects the age at maturity of their offspring. It is based on two components which he documented, (1) the strong correlation between female age and her body size, and (2) the effect of female size on the size, growth rate, and subsequent age at maturity of her offspring. For Skeena River sockeye, Bilton (1971) showed the following. Egg weight was significantly correlated with body length of female spawners ($r = 0.79$, $P<0.01$), irrespective of spawner age. In addition, weight of 3-month-old fry was correlated with both the weight of their eggs ($r = 0.96$, $P<0.001$) and length of their female parents ($r = 0.71$, $P<0.01$). These correlations became weaker for 9-month-old fry, but they were still positive ($r = 0.47$, $P = 0.14$ for egg weight; $r = 0.595$, $P = 0.054$ for female length). However, statistical power (probability of rejecting the null hypothesis) in the case of 9-month-old fry was low because of the small sample ($N = 11$ females). Bilton hypothesized that if the size advantage of large eggs persisted throughout the rest of freshwater life, then smolts produced from these large fry (and large females) would be larger than smolts from small females (Fig. 1F). Although this relation has never been tested for sockeye, Fraser et al. (1983) found a significant positive correlation between the size of coho smolts (*O. kisutch*) and size of their female parents from Big Qualicum River, B.C. ($r = 0.79$, $P<0.01$). The well known inverse relation between smolt size and ocean age at maturity noted in the previous section (Fig. 1G) would therefore cause offspring from large (old) females to mature at a relatively young ocean age. Thus, in



MODIFIED BILTON
BILTON
A)
Fry size (g)
B
A
A
B
Ocean age of ♀ parents (yr)
E)
Fry size (g)
B
A
A
B
Ocean age of ♀ parents (yr)
B)
Smolt age (yr) or size (g)
A
B
A
B
Fry size (g)
F)
Smolt size (g)
B
A
A
B
Fry size (g)
C)
Ocean age of offspring (yr)
B
A
B
A
Smolt age (yr) or size (g)
G)
Ocean age of offspring (yr)
A
B
A
B
Smolt size (g)
D)
Ocean age of offspring (yr)
B
A
A
B
Ocean age of ♀ parents (yr)
H)
Ocean age of offspring (yr)
A
B
A
B
Ocean age of ♀ parents (yr)

FIG. 1. Schematic illustration of the steps which link mean ocean age of a population of female parents to mean ocean age of their offspring under two hypothesized mechanisms. All variables on the X and Y axes are means for a population. Right column covers Bilton's (1970, 1971) maternal effects hypothesis and left column refers to our modified Bilton hypothesis for stocks in which two ages at smolting exist. Smallest sizes and youngest ages are at the origin in all graphs. A and B on axes are explained in text.

contrast to the first two mechanisms, Bilton's maternal effects, if acting alone, would lead to an inverse correlation between ocean age of female spawners and ocean age at maturity of their offspring (Fig. 1H). Female spawners with mean ocean age symbolized as "B" in Fig. 1E would produce offspring with mean fry size, smolt size, and ocean age at maturity also symbolized as "B" in Fig. 1E–1G, giving the net result shown in Fig. 1H. Alternatively, if ocean age were also genetically heritable, then the positive correlation between parent and offspring age at maturity caused by the heritable mechanism would tend to offset the negative correlation caused by Bilton's maternal effects (Fig. 1H), but only for correlations involving female parents (by definition, male parents do not cause a maternal effect because they do not affect egg size). The regression of mean ocean age of offspring on mean ocean age of female parents would thus have a smaller slope than the regression on male parent age.

MODIFIED BILTON HYPOTHESIS

This mechanism is an extension of Bilton's maternal effects hypothesis to stocks in which more than one smolt age commonly exists. This applies to a large fraction of British Columbia and Alaska sockeye stocks. Our hypothesized modified Bilton mechanism has the same initial component as Bilton's maternal effects mechanism, namely, that emergent fry size should be positively correlated with ocean age of their female parents (Bilton 1970, 1971; Fig. 1A). However, our hypothesis differs at the next stage because in some stocks, growth during the first summer in the lake can affect the length of the lake residence period. For the Wood River system in Alaska, the proportion of fish that remained in the lake for an extra year was negatively correlated with fry size at the end of the first summer ($r = 0.62$, $P = 0.01$, $N = 16$; data from Rogers 1975). Faster growing fish tend to go to sea during the second summer of lake residence while slower growing fish migrate during the third summer (Krogius 1960; Burgner 1962; Ricker 1972), creating an inverse relation between fry size and smolt age (Fig. 1B). In stocks with more than one smolt age, fish from the same brood which smolt one year later than their cohorts are about 60% heavier at smolting (e.g. Rogers 1984, his table 2). The smallest fry would therefore be expected to produce the largest smolts. In Bilton's hypothesis, only one smolt age was considered possible, so fry size did not affect smolt age, and fry size and smolt size were positively correlated (Fig. 1F). Finally, the inverse relation between mean smolt size (or age) and mean ocean age at maturity described above results in larger (older) smolts maturing at a younger ocean age (Fig. 1C) (Koo 1964; Rogers 1984, 1987). By tracing through this sequence of three components of our modified Bilton hypothesis, relatively old female spawners (marked by B in Fig. 1D) will produce offspring which also mature at an old ocean age. Similarly, young female spawners (marked A in Fig. 1D) will produce offspring which mature at an early ocean age.

Our modified Bilton hypothesis therefore predicts a positive correlation between mean ocean age of female parents and that of offspring, but the hypothesis does not imply that the trait is directly heritable genetically. Rather, ocean age is indirectly determined through the combination of the somatic or maternal effects of female parent size on fry size documented by Bilton, and through the two inverse relationships between fish size and duration of the lake and ocean life history stages. These latter inverse relations are most likely genetically determined, and fixed within a population as a result of selection for optimal responses to varying environments. It therefore may be sufficient to use our modified Bilton mechanism, which is largely a physiological explanation, rather than invoking additive genetic variance, to explain the correlations across years between mean ocean ages of parents and their offspring.

We tested whether the modified Bilton mechanism proposed here is a sufficient explanation of the correlations between mean ocean age of offspring and their parents in British Columbia and Bristol Bay, Alaska, sockeye stocks.

Methods

DATA SOURCES

We use the Gilbert–Rich notation for fish ages where the larger number indicates the year of life when the fish returned to spawn and the subscript is the year of life when the fish entered the ocean. In this paper "sub-2" and "sub-3" refer to fish which have smolted in their second or third year of life, respectively.

Data on abundances of nine Bristol Bay, Alaska, sockeye stocks (Branch, Egegik, Igushik, Kvichak, Naknek, Nuyakuk, Togiak, Ugashik, and Wood River systems) covered the years 1957–1978, and were stratified by age, smolt type, and sex for both catch and escapement (Yuen et al. 1981). Mean annual spawner lengths (mideye to fork of tail) for each age group and sex for these stocks were also drawn from Yuen et al. (1981). Smolt length and weight data for three Bristol Bay stocks were from Eggers and Yuen (1984).

The major age-groups 4_2, 5_2, 5_3 and 6_3 comprise an average of 97.8% of Bristol Bay sockeye returns. These data include estimated high-seas catches of maturing fish (provided by C. P. Meacham, ADFG, Anchorage, AK, pers. comm.), allocated to each stock and age in proportion to the relative total returns.

Total sockeye returns and escapements (sexes combined) for the Babine Lake, British Columbia stock were from C. West (pers. comm., Canada Dep. of Fisheries and Oceans (DFO), Vancouver) and L. Jantz (pers. comm., DFO, Prince Rupert, B.C.) for the 1956–1977 brood years. Return abundances included commercial and native Indian catches and escapements. Babine sockeye are nearly all sub-2 fish, and mature at ages 3_2, 4_2 and 5_2.

MEAN AGES

Mean ages of the population of parent spawners were calculated from annual abundance data on escapements for each stock. Mean age of the offspring from each brood year was calculated from the total returns (catch plus escapement). For Bristol Bay stocks, parent and offspring data were stratified by sex, and the weighted mean smolt age and ocean age were calculated for each brood year from the weighted abundances at each age (summarized in Table 1). We used

TABLE 1. Means ($\bar{x}$) and standard deviations (SD) of age measures for nine Bristol Bay stocks used to test the modified Bilton hypothesis.

	Ocean age						Smolt age			
	Female spawners		Male offspring		Female offspring		Male offspring		Female offspring	
Stock	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Branch	2.35	0.30	2.37	0.31	2.42	0.18	2.20	0.20	2.22	0.24
Egegik	2.39	0.27	2.39	0.16	2.48	0.16	2.87	0.09	2.88	0.09
Igushik	2.60	0.22	2.62	0.14	2.62	0.15	2.24	0.19	2.27	0.22
Kvichak	2.25	0.23	2.19	0.14	2.16	0.07	2.80	0.17	2.83	0.17
Naknek	2.51	0.30	2.44	0.17	2.58	0.16	2.62	0.18	2.63	0.19
Nuyakuk	2.73	0.30	2.83	0.08	2.85	0.09	2.09	0.07	2.11	0.09
Togiak	2.57	0.25	2.63	0.15	2.68	0.12	2.21	0.11	2.21	0.10
Ugashik	2.33	0.34	2.29	0.14	2.39	0.16	2.64	0.25	2.66	0.26
Wood	2.35	0.24	2.46	0.20	2.43	0.19	2.14	0.12	2.14	0.13

all data available, but because data were not collected for all years for each stock, the length of the data series for the nine Bristol Bay stocks ranged from 8 to 15 years.

We calculated only the sexes-combined mean ocean age for parents and offspring of the Babine stock, as there was no variation in smolt age.

TIME TRENDS

To test for the existence of time-trends in the data that might confound our interpretations, all variates were regressed against time using simple linear regressions. For Bristol Bay stocks, of the 36 regressions of offspring ages (2 sexes × 2 age measures × 9 stocks), two were significant at $\alpha = 0.05$ (Togiak male and female ocean age). Here and in other cases in this paper where a number of regressions were done, a binomial test was used to determine whether the number of significant regressions obtained was more than would be expected by chance alone. Two of 36 regressions is not more than would be expected by chance at $\alpha = 0.05$ ($P = 0.73$, National Bureau of Standards 1952). One of 18 time trends in mean ocean age of parents was significant (Kvichak female), as was one of nine time trends in female spawner abundance (Branch; abundances were used in analysis described below). Probabilities associated with obtaining these results by chance were 0.60 and 0.93, respectively. There were no significant time trends with the Babine age measures. Because the number of significant time trends in our data were not more than would be expected by chance alone, we used the raw data in subsequent analyses, rather than time-trend residuals.

PARENT–OFFSPRING CORRELATIONS

Peterman (1985) reports a significant tendency in Bristol Bay sockeye for mean ocean age of offspring to be positively correlated with mean ocean age of their parents. His correlations were done with mean ages for all sexes combined, but in this analysis, we calculated separate correlations between ocean ages of male offspring and ocean ages of female parents, and similar correlations between female offspring and female parents.

A single sexes-combined parent–offspring regression was calculated for Babine sockeye, as sex-specific abundance data were not available.

MODIFIED BILTON HYPOTHESIS

We tested whether the modified Bilton hypothesis could provide an alternative explanation to genetic inheritance for the observed positive correlations between ocean ages of parents and offspring in Bristol Bay sockeye. We did this by examining data on the components of the hypothesis.

Determinants of Smolt Age

We first tested whether mean age at smolting of offspring was inversely related to mean ocean age of their female parents, as is predicted by combining the first two subcomponents of the hypothesis, shown in Fig. 1A and 1B. We were not able to test each subcomponent separately because of the lack of extensive fry size data, so instead we examined data relating female parent age to offspring smolt age.

The maternal effects mechanism which leads to the predicted inverse relation between age of female parents and age at smolting of their offspring is conditional upon a correlation between female adult age and her body size. We therefore estimated this correlation for the subset of years in which both mean body sizes and ages were available.

Because fry growth has been shown to affect the age of smolting (Ricker 1972) and fry abundance can affect fry growth (Burgner et al. 1969; Rogers 1973), we used multiple regression to test for the effect of size of female parents and fry density on smolt age. The lack of fry abundance data forced us to assume that potential egg deposition (PED) was linearly related to fry abundance. PED for each brood year was the product of the average fecundity per female and the number of female spawners. Average fecundity was calculated from a length–fecundity relationship using mean length of female spawners in each brood year. Length-specific fecundity relations were available only for the Wood (D. Rogers, University of Washington, Seattle, WA, pers. comm. 1984) and Kvichak (Mathisen and Gunnerod 1969) stocks. A single relation, used for all Bristol Bay stocks, was derived by averaging the coefficients of the available equations, which were surprisingly similar for the two stocks. The resulting equation was:

$$F = -1713 + 10.83\ L$$

where F is fecundity, and L is mideye–tail fork length (mm). The multiple regression of smolt age used was:

$$S = b_0 + b_1\ P + b_2\ \text{PED},$$

where S is offspring smolt age, P is mean ocean age of female parents and PED is the potential egg deposition of those females. Separate regressions were calculated for each stock and sex of offspring.

Determinants of Ocean Age

The second component of the modified Bilton hypothesis which we tested was the inverse relation between mean ocean age of fish of a given brood year and their smolt age (Fig. 1C). For each stock and sex, ocean ages of offspring were regressed on their smolt ages.

The modified Bilton hypothesis could not be tested for the Babine stock because nearly all fish smolted as sub-2s.

TABLE 2. Regressions (b = slope) of mean ocean age of offspring on mean ocean age of female spawners, with offspring separated by sex, for nine Bristol Bay sockeye stocks. N = number of years of data, r^2 = the coefficient of determination, and P = the probability that $b = 0$. Asterisks highlight significant regressions.

		Male offspring on female spawners			Female offspring on female spawners		
Stock	N	b	r^2	P	b	r^2	P
Branch	10	0.07	0.02	0.68	0.17	0.07	0.45
Egegik	15	0.41	0.45	0.01 *	0.32	0.29	0.04 *
Igushik	9	0.37	0.35	0.09	0.36	0.29	0.14
Kvichak	13	0.27	0.22	0.11	0.09	0.09	0.32
Naknek	12	0.39	0.46	0.02 *	0.33	0.35	0.04 *
Nuyakuk	8	0.18	0.44	0.07	0.25	0.57	0.03 *
Togiak	8	−0.06	0.02	0.76	−0.04	0.04	0.64
Ugashik	14	0.33	0.57	0.002*	0.38	0.58	0.002*
Wood	9	0.40	0.32	0.11	0.50	0.38	0.08

TABLE 3. Multiple regressions of mean age at smolting of offspring on mean ocean age of female parents (b_1) and potential egg deposition (in 10^{10} eggs, b_2) for nine Bristol Bay sockeye stocks. Results are separated by sex of offspring. Asterisks highlight significant cases; N = sample size in years.

		Overall regression			Parent age		Potential egg deposition	
Stock	N	Mult. r^2	P	b_0	b_1	$P_{b_1=0}$	b_2	$P_{b_2=0}$
				Male smolt age				
Branch	10	0.19	0.48	2.72	−0.23	0.40	0.39	0.70
Egegik	15	0.40	0.047 *	3.27	−0.19	0.037 *	0.22	0.06
Igushik	9	0.64	0.045 *	2.89	−0.37	0.17	5.29	0.018*
Kvichak	13	0.01	0.96	2.75	0.01	0.95	0.01	0.79
Naknek	12	0.35	0.15	3.55	−0.37	0.08	−0.08	0.87
Nuyakuk	8	0.80	0.018 *	2.46	−0.16	0.023 *	1.94	0.013*
Togiak	8	0.17	0.62	2.65	−0.20	0.39	3.11	0.45
Ugashik	14	0.49	0.024 *	3.93	−0.53	0.008 *	−0.46	0.39
Wood	9	0.45	0.17	3.03	−0.34	0.07	−0.47	0.48
				Female smolt age				
Branch	10	0.14	0.59	2.77	−0.24	0.48	0.41	0.75
Egegik	15	0.35	0.08	3.24	−0.17	0.053	0.18	0.10
Igushik	9	0.66	0.039 *	3.11	−0.47	0.14	6.23	0.016*
Kvichak	13	0.07	0.68	3.29	−0.20	0.44	−0.001	0.99
Naknek	12	0.46	0.06	3.66	−0.42	0.047 *	0.06	0.91
Nuyakuk	8	0.96	0.0002*	2.86	−0.29	0.0001*	1.67	0.002*
Togiak	8	0.22	0.53	2.59	−0.18	0.38	3.64	0.33
Ugashik	14	0.45	0.039 *	3.91	−0.53	0.013 *	−0.34	0.55
Wood	9	0.29	0.35	2.98	−0.34	0.17	−0.23	0.80

TABLE 4. Regressions (b = slope) of mean ocean age of offspring on mean smolt age of offspring, by sex. Asterisks highlight significant regressions.

		Male			Female		
Stock	N	b	r^2	P	b	r^2	P
Branch	11	0.05	0.01	0.82	0.10	0.02	0.69
Egegik	15	−1.02	0.35	0.02 *	−0.82	0.20	0.10
Igushik	11	−0.34	0.19	0.17	−0.39	0.30	0.08
Kvichak	13	−0.21	0.07	0.37	−0.14	0.12	0.26
Naknek	13	−0.43	0.19	0.13	−0.38	0.19	0.13
Nuyakuk	11	−0.40	0.10	0.34	−0.60	0.37	0.046*
Togiak	9	0.26	0.03	0.64	−0.15	0.01	0.75
Ugashik	15	−0.45	0.61	0.001*	−0.46	0.55	0.002*
Wood	12	−0.33	0.04	0.55	0.14	0.01	0.77

Results

PARENT–OFFSPRING CORRELATIONS

Mean ocean ages of offspring tended to be positively correlated with the mean ocean age of their female parents for the Bristol Bay stocks (Table 2). For each sex of offspring, 8 of 9 slopes were positive; the probability of obtaining this result by chance alone if the variables were in fact uncorrelated is 0.039 (signs test). In addition, the probability of obtaining by chance alone, 4 of 9 significant female regressions at $\alpha = 0.05$ is 0.001; for males the probability of obtaining 3 significant regressions out of 9 is 0.008. This analysis differs from that of Peterman (1985) in two ways: (1) we used raw data rather than time trend residuals, and (2) separate regressions were calculated for each sex of offspring. Nonetheless, the results are similar, with the significant regressions arising from the same stocks in both analyses.

The Babine sexes-combined offspring-on-parent ocean age regression was positive and highly significant ($r^2 = 0.35$, $P = 0.004$, $N = 22$).

MODIFIED BILTON HYPOTHESIS

Determinants of Smolt Age

Mean length of female spawners was positively and highly significantly correlated with mean female ocean age in all nine Bristol Bay sockeye stocks (all $P<0.001$). Therefore, the more extensive data on mean female ages which we used adequately reflected the effects of size of females on their offspring.

Mean smolt age of offspring of some Bristol Bay stocks was correlated with both ocean age of female parents and potential egg deposition. For each sex of offspring, more multiple regressions were significant than would be expected by chance alone (males: $^4/_9$, $P = 0.0006$; females $^3/_9$, $P = 0.008$, Table 3). The independent variables of the multiple regression were not significantly correlated in any of the nine stocks. Partial regression coefficients for ocean age of female parents were significant in four stocks, Egegik, Nuyakuk, Ugashik, and Naknek (Table 3). The signs of the coefficients in the multiple regressions generally followed the hypothesized directions; signs of the coefficient for female spawner ocean age were negative in 8 of 9 male and 9 of 9 female regressions. Therefore, when juvenile abundance is taken into account, ocean age of female parents does in some cases have a significant inverse effect on age of smolting of their offspring.

Determinants of Ocean Age

Ocean age of offspring was significantly negatively correlated with their age at smolting in 2 of 9 cases for each sex (Table 4, P of obtaining this result = 0.07). The signs of the correlations were negative in 7 of 9 cases for each stock, although this result is not significantly different from an equal frequency of + and − signs ($P = 0.18$).

Components Combined

In order for the modified Bilton mechanism to produce positive offspring-on-parent ocean age correlations in a given stock, both components of the mechanism must be operating. Of the seven significant parent–offspring ocean age regressions shown in Table 2, in four cases, Ugashik male and female, Nuyakuk female, and Egegik male, both components of the modified Bilton mechanism were significant (Table 5). Thus, in over half of the cases where a significant parent–offspring correlation was observed, there is good evidence that the modified Bilton mechanism is a viable alternative. In addition, for the Egegik female case, the significance levels of both components were less than 0.1. In the Naknek case, one of the modified Bilton components was significant, and the signs of the other components were consistent with the hypothesis.

Data for the combined components of our modified Bilton mechanism are shown for Ugashik River female sockeye in Fig. 2–4, as an example. Figure 2 corresponds to the sum of Fig. 1A and 1B, Fig. 3 shows data supporting the component given in Fig. 1C, and Fig. 4 shows that combining relations in Fig. 2 and 3 can result in a positive correlation between ocean ages of female parents and those of their offspring, as predicted in Fig. 1D.

Discussion

MODIFIED BILTON HYPOTHESIS

The empirical support for the modified Bilton hypothesis means that the positive correlations of offspring and parent

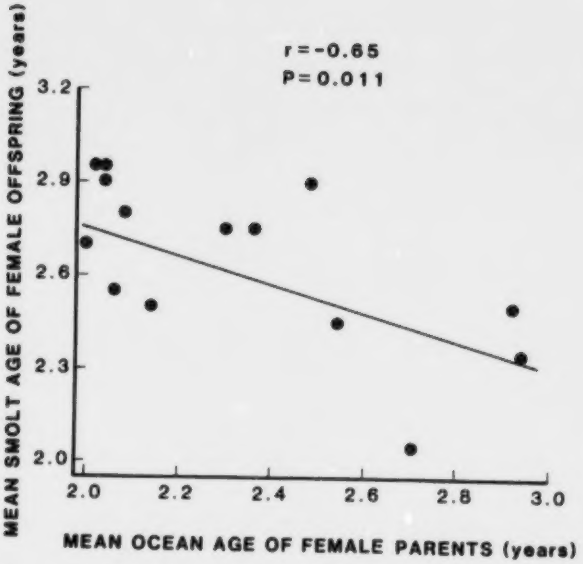


FIG. 2. Relation between mean ocean age of smolting of female offspring and the mean ocean age of their female parents, for Ugashik River sockeye salmon. Each data point represents one brood year for brood years 1958–71.

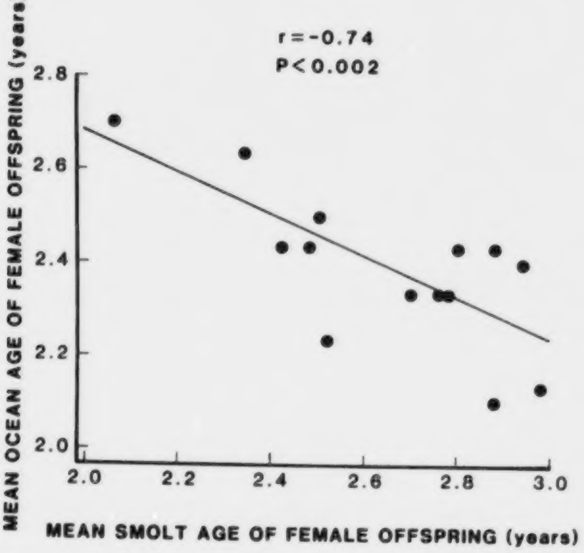


FIG. 3. Relation between mean duration of ocean life and mean age at smolting for female Ugashik River sockeye salmon; one data point per brood year.

ocean ages found by Rogers (1984, 1987) and Peterman (1985) for Bristol Bay sockeye stocks cannot necessarily be taken as evidence of direct genetic inheritance of ocean age. There is good evidence that in some Bristol Bay stocks the observed offspring–parent ocean age correlations could be the result of our alternative hypothesis, which is based mainly on physiological mechanisms.

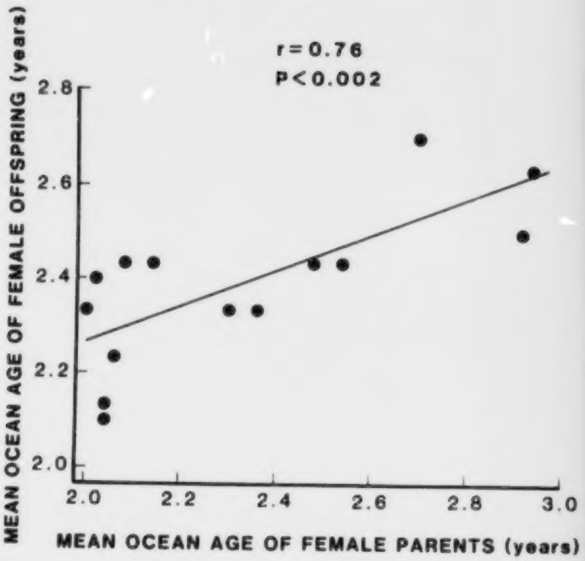


FIG. 4. Relation between mean ocean age of female offspring and the mean ocean age of their female parents, for Ugashik River sockeye salmon; one data point per brood year.

A reason that the patterns of age at maturity in other stocks are not explainable by the modified Bilton hypothesis is because of differences among stocks in the degree to which other variables affect the maturation process. For example, in the Igushik stock, smolt age of male and female offspring was significantly correlated with the indirect measure of fry density (potential egg deposition), but not with ocean age of parents (Table 3). This dominating influence of fry density is not surprising, given that the Igushik stock had the highest mean density (4 360) of spawners per km^2 surface area of rearing lake of any of the Bristol Bay stocks considered (Burgner et al. 1969). A density-dependent growth effect may have overwhelmed any parental size effect on smolt age, making it unlikely that the modified Bilton mechanism which we hypothesized would be observed.

Other variables also affect to varying degrees the second component of the modified Bilton hypothesis, the inverse correlation between age at smolting of offspring and their subsequent duration in the ocean. Our ability to detect a correlation between these two variables is implicitly based on a positive correlation between smolt age and smolt size, resulting in larger (older) smolts maturing earlier. The Ugashik stock, which showed the strongest inverse correlation between mean smolt age and mean ocean age (Table 4), also had the highest correlation between smolt age and smolt weight ($r = 0.86$, $P = 0.0003$). The only other stocks for which we had mean smolt size and age data, Naknek and Kvichak, had weaker smolt age and size correlations ($r = 0.62$, $P = 0.008$; $r = 0.50$, $P = 0.028$, respectively) and these failed to show significant inverse correlations between smolt age and ocean age (Table 4). In these latter cases, the influence of environmental sources of variability on smolt size or age may have obscured the relation between smolt age and ocean age and the modified Bilton hypothesis cannot be demonstrated with these data.

In spite of these other factors, though, four of the seven cases in which there were significant positive correlations between ocean age of female parents and offspring also had

TABLE 5. Summary of regressions reported in Tables 2–4 pertaining to the modified Bilton hypothesis. For each sex of offspring, columns from left to right refer to regressions of offspring ocean age on female parent ocean age, offspring smolt age on female parent ocean age, and offspring ocean age on smolt age. Significance levels indicated as: ** $P<0.01$; * $0.01 \leq P<0.05$; ? $0.05 \leq P \leq 0.10$, — $P>0.1$.

	Male offspring			Female offspring		
Stock	Offspring-parent ocean ages	Offspring smolt-parent ocean ages	Offspring ocean-offspring smolt ages	Offspring-parent ocean ages	Offspring smolt-parent ocean ages	Offspring ocean-offspring smolt ages
Branch	—	—	—	—	—	—
Egegik	*	*	*	*	?	?
Igushik	?	—	—	—	—	?
Kvichak	—	—	—	—	—	—
Naknek	*	?	—	*	*	—
Nuyakuk	?	*	—	*	**	*
Togiak	—	—	—	—	—	—
Ugashik	*	**	**	*	*	**
Wood	—	?	—	?	—	—

significant correlations in both components of the modified Bilton hypothesis (Table 5). A fifth case (Naknek female offspring) showed one component significant. There is thus strong evidence that our hypothesis may explain the interannual variability in ocean age at maturity in some stocks.

We may have underestimated the number of significant inverse partial correlations between smolt age and age of their female parents. Our model could have been refined considerably if annual data on egg size and total fry abundance had been available for each brood year and stock. Errors in the independent variables in regressions tend to bias the estimated slope toward zero, reducing the power of detecting a significant relation (Ricker 1973).

ENVIRONMENTAL TRENDS

The significant correlations between mean ocean ages of parents and their offspring which are explainable by the modified Bilton hypothesis are explainable by environmental influences only if there is a long-term directional time trend in the environment which would cause a parallel trend in the age variates. Of the few significant time trends in parent or offspring smolt and ocean ages, none was associated with any of the seven significant parent–offspring correlations of Table 2, indicating that an environmental mechanism was probably not responsible for the parent–offspring correlations.

GENETIC INHERITANCE MECHANISM

In two of the stocks examined there is indirect evidence for the genetic inheritance of ocean age at maturity. The Naknek stock had significant parent–offspring correlations in mean ocean age, but the components of the modified Bilton hypothesis were weak, and environmental time trends did not exist. Our Babine Lake results, as well as those covering that stock over an earlier period (Larkin and MacDonald 1969), also demonstrated a significant positive parent–offspring correlation which did not have time trends, and because this stock has only one smolt age, the modified Bilton hypothesis does not apply. In these cases, genetic inheritance is therefore the most likely one to explain interannual variation in ocean age.

There was little difference between sexes in any of our results, suggesting that the factors influencing year-to-year variation in age at maturity are not sex-specific. In fact, the smolt ages of male and female offspring were highly positively correlated among years in all Bristol Bay stocks, as were ocean ages (all $P \leq 0.01$). *Mean* ages at maturity, however, are sex-specific; males tend to mature earlier than females (Rogers 1980).

MATERNAL EFFECTS

Our results do not support Bilton's (1971) original maternal effects hypothesis. That hypothesis predicted an inverse relationship between ocean age of female parents and ocean age of offspring, opposite to the relationship observed for the Babine and eight Bristol Bay stocks (Table 2). The only negative regression slope was very weak (Togiak, $b = -0.06$ for male offspring, -0.04 for female offspring; $P>0.6$ for both).

Our sex-specific data on population mean ages could, in theory, be used to estimate the relative importance of the genetic, Bilton's maternal effect, and our modified Bilton hypothesis. The maternal effects mechanism alone should result in the slope of the female parent–offspring mean ocean age regression being lower than the slope using male parents. In contrast, our modified Bilton hypothesis predicts that the slope of offspring ocean age on male parent age should be lower than that on female age because male parents do not influence the age at smolting of their offspring. Comparison of these slopes is informative only if mean ages of the different sexes are uncorrelated. Unfortunately, male and female spawner ages were highly positively correlated in our stocks (all $P<0.001$), rendering the various mechanisms inseparable. As a result, regressions of mean ocean age of male or female offspring on male parent ocean age were similar to the regressions involving female parent ocean ages shown in Table 2.

MANAGEMENT IMPLICATIONS

Size-selective fishing gear has the potential to exert directional selection (Ricker 1982; Killick and Clemens 1963) on ocean age at maturity because ocean age and size at maturity are highly correlated, as noted above. However, the response of a population to size-selective fishing will depend on the mechanisms which control the interannual variation in ocean age at maturity. For those stocks in which offspring ocean age may be heritable (perhaps Naknek and Babine Lake), size-selective fishing could alter the frequencies of genes affecting ocean age, changing the mean ocean age and reducing the genetic variance for that trait. The reduction in genetic variance would slow the return of the stock to its original state upon the elimination of size-selective fishing.

In stocks where the modified Bilton mechanism operates, size-selective fishing will produce initial responses similar to a stock in which variation in age at maturity is genetically controlled. Selective removal of larger (greater ocean age) fish, for example, will result in smaller spawners, which will in turn tend to produce smaller fry. These fry will smoltify at an older age, and will spend less time in the ocean than before size-selective fishing. However, in contrast to stocks controlled by a heritable ocean age, this change in ocean age would be phenotypic only, and the stock would more rapidly return to its former mean ocean age at maturity after the cessation of selective fishing. Long-term selective fishing may eventually alter the genetically controlled relationships between fry size and smolt age, and smolt age and ocean age.

RECOMMENDED EXPERIMENTS

For a particular stock, it is not possible to distinguish between the modified Bilton and genetic hypotheses with the population data that we used. An experimental approach is required to estimate the relative importance of these alternatives in explaining the observed correlations in ocean age. Even though Bilton's (1971) experiments failed to show a significant relation between size of 9-month old fry and either egg size or size of female parents, we have shown that smolt age is inversely correlated with female size. Therefore, the maternal size effect does carry through to the smolt stage in some of our stocks. The exact mechanism causing the effect of parent size on smolt age could be elucidated by rearing through to smolting, fry from various sizes of eggs and parents. This is an extension of the experiments of Bilton (1970) and Beacham et al. (1985). The genetic heritability of ocean age at maturity could be tested by a breeding experiment using similarly sized females of different ages, to control for the influence of female size on egg size (Bilton 1971). Only after such experiments are done will we be able to draw conclusions concerning the long-term effects of size-selective fishing.

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Migratory Structure of the Kvichak River Sockeye Salmon (*Oncorhynchus nerka*) Escapement, 1983

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Abstract

JENSEN, K. A., AND O. A. MATHISEN. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983, p. 101–109. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Sockeye salmon (*Oncorhynchus nerka*) in the 1983 Kvichak River spawning escapement were tagged during seven sequential periods. Recovery surveys were conducted on all known spawning grounds in the watershed to determine the migratory structure of various escapement components. The period of peak spawning varies among habitats and occurs from early August to mid-October. Recoveries from every tagging period were made in every geographic area, on every type of spawning bed, and from each temporal (early, middle, and late) spawning component. The Newhalen River–Lake Clark complex had a greater proportion of early migrants than did Iliamna Lake. However, neither the estimated mean of migratory time density or its associated variance differed significantly among various escapement components. Recoveries from schooling/spawning fish and from spent fish in three rivers indicated an overlap in the time of migration of the two groups. Live unspawned and spawning fish tagged during the first two tagging periods were mingled with spent and dying fish tagged in period 4 or later. The minimum time span of active spawning of salmon from a given tagging period ranged from 30 to 70 days. Tags from every period were observed on actively spawning fish during a 20-day span. The results showed the potential for genetic mixing between migrants from every portion of the escapement.

Résumé

JENSEN, K. A., AND O. A. MATHISEN. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983, p. 101–109. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Des saumons nerkas (*Oncorhynchus nerka*) de la remontée de frai de 1983 de la rivière Kvichak ont été marqués au cours de sept périodes consécutives. Des relevés par récupération d'étiquettes ont été réalisés dans toutes les frayères connues du bassin versant afin de déterminer la structure migratoire des diverses composantes de la remontée. Le pic de la période de frai variait selon les habitats et était noté du début d'août à la mi-octobre. Des étiquettes de chaque période de marquage ont été récupérées dans toutes les zones géographiques, dans tous les types de frayères et pour chaque composante de frai (hâtive, moyenne et tardive). On a noté une plus grande proportion de géniteurs hâtifs dans le complexe rivière Newhalen – lac Clark que dans le lac Iliamna, mais la moyenne estimée de la densité migratoire en fonction du temps et sa variance ne différaient pas de façon significative entre les diverses composantes de la remontée. La récupération d'étiquettes provenant de poissons regroupés ou en frai et de poissons ayant déjà frayé dans les trois cours d'eau indiquait un recoupement des moments de migration des deux groupes. Des poissons n'ayant pas encore frayé et des poissons en train de frayer marqués au cours des deux premières périodes d'étiquetage étaient mêlés à des poissons ayant déjà frayé et à des poissons moribonds qui avaient été marqués au cours de la 4^e période ou d'une période subséquente. La durée minimale de frai actif des saumons d'une période de marquage donnée variait de 30 à 70 jours. On a noté la présence, pendant 20 jours, de poissons en frai actif qui avaient été marqués pendant chacune des périodes d'étiquetage. Les résultats indiquent qu'il y a possibilité de mélange génétique entre les géniteurs de chaque composante de la remontée.

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Introduction

The historical management strategy for sockeye salmon (*Oncorhynchus nerka*) runs based on numerical reproduction models has recently been expanded to include additional factors such as the type of spawners reserved for reproduction. Spawners have different freshwater and ocean ages and times of migration and spawning. Therefore, to preserve diversity, a proportionate escapement should be obtained from every segment and age-group of a run. Quantitatively, migratory timing can be described by a probability distribution with its specific mean and variance. Kapuscinski (1984) stated that the long-term survival of a stock was more dependent on the maintenance of an adequate degree of variance of fitness around the mean than simply on the value of mean fitness because the stock must be able to adapt to changing environmental conditions. An additional concern is the ability of a highly efficient fishery to drastically perturb the temporal distribution of the escapement. Thus it becomes vital to reserve adequate escapement from all temporal run components as well as all spawning populations within the system and to maintain sufficient genetic diversity within individual populations.

Stock separation investigations employing tagging and other techniques have demonstrated differential timing of sockeye salmon races returning to a number of river systems. Sockeye salmon enter the Fraser River from late June through September, and individual races exhibit great differences in timing with peak entry dates ranging from early July for the early Stuart run to mid-September for the Adams River run. The chronological order of migration remains largely unchanged between passage from the commercial fishery near the river mouth and spawning hundreds of kilometres upstream (Killick 1955). Substantial differences in migratory timing exist among stocks originating in different tributaries of the Skeena River, British Columbia (Takagi and Smith 1973) and the upper Copper River, Alaska (Merritt and Roberson 1983). The Russian River, Alaska, has distinct early and late runs that have mean entry dates a month apart and spawn in different areas (Nelson 1984). The two major spawning groups of the Chignik River, Alaska, have peaks in migration just over 3 weeks apart (Dahlberg 1968) and, therefore, can be managed separately to achieve optimum production from both stocks.

The purpose of this study was to describe in detail the migratory structure of sockeye salmon in the Kvichak River system of Bristol Bay, Alaska. The results of previous tagging studies on this system did not demonstrate any pronounced segregation in time of passage of the various races at their entry into Iliamna Lake, the major nursery area of the Kvichak River (Smith 1964). Verification was needed because of the commercial importance of the system and the greatly increased level of sockeye salmon production in Bristol Bay in general in recent years.

Materials and Methods

STUDY AREA

The Kvichak River watershed on the northeast side of Bristol Bay covers an area of approximately 19 700 km^2 (Fig. 1). It includes two major lakes, Lake Clark (370 km^2) and Iliamna Lake (2 622 km^2), which are connected by the Newhalen River. The Newhalen River originates in Six-Mile Lake, is approximately 38 km long, and drains the Lake Clark watershed into Iliamna Lake approximately 80 km east of Igiugig. Iliamna Lake discharges at Igiugig through its 90 km long trunk stream, the Kvichak River, into eastern Bristol Bay. The watershed contains more than 100 discrete spawning areas which include large rivers, tundra, glacial, and clear streams, island and mainland beaches, and spring-fed ponds. A visual counting station which provides an estimate of daily escapement into the entire system is maintained at Igiugig by the Alaska Department of Fish and Game (ADF&G). The Lake Clark escapement is estimated at another counting station maintained by the Fisheries Research Institute (FRI) at RM (river-mile) 21 on the Newhalen River.

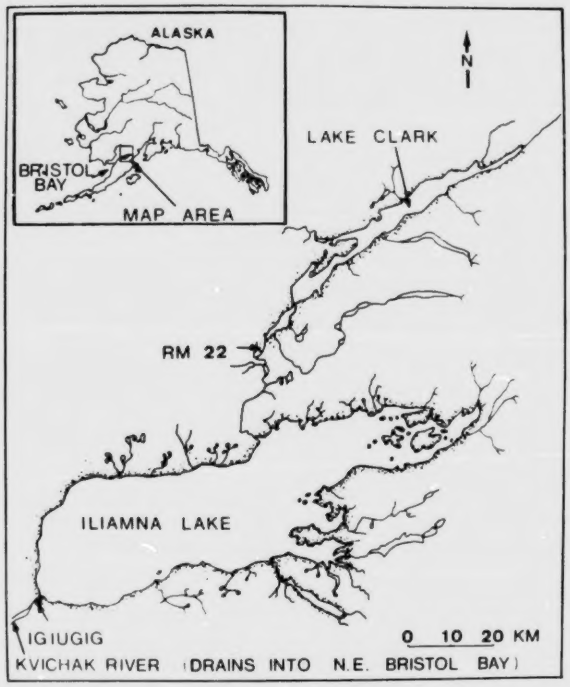

FIG. 1. The study area (Kvichak River drainage) in Bristol Bay, Southwest Alaska, with sockeye salmon counting stations at Igiugig and at RM (river-mile) 22 Newhalen River.

TIME OF SPAWNING AND AGE STRUCTURE

The dates of peak spawning vary among spawning areas and occur from early August to mid-October. Time of spawning for individual stocks is governed by the temperature regimes on the spawning grounds so that fry emergence and the beginning of external feeding occur during the optimum periods for survival (Olsen 1964). Lake residence is generally 1 or 2 years and ocean residence is 2 or 3 years. Combinations of other fresh-and saltwater age-groups generally contribute less than 2% to the total escapement. All major age-groups are found simultaneously on the spawning grounds. This enhances the potential for genetic diversity of the races, and provides for long-term stability by including at least three consecutive brood years in any year's spawning population.

TAGGING

Sockeye salmon were captured, tagged, and released at Igiugig near the outlet of Iliamna Lake (Fig. 1) from June 28 to July 19, 1983. Salmon were captured at three sites by beach seining and at a fourth site in a beach seine trap. The beach seine was 46 m × 3.6 m of 76 mm stretch mesh and was set from a boat by the standard round-haul technique. The trap was 122 m × 3.6 m of 76 mm stretch mesh seine. The upstream end was staked onshore, and the upstream corner was attached to an anchor-supported steel stake driven into the bottom approximately 15 m offshore. The remaining 100 m of seine trailed downstream with the current, forming an enclosure of approximately 167 m^2. When fish were visible in the trap, the net was slackened from the corner stake, and the downstream end was pulled to shore with the boat, thus trapping the fish. Fish from small sets were transferred to live boxes; tagging commenced when approximately 250 fish had been captured. Fish were tagged directly from the seine when more than 200 were captured in a single set. One to three people handled fish, one person tagged fish, and one person recorded data. Fish were captured throughout the day and from both sides of the river.

Floy internal-anchor tags were applied to the left side of the salmon, through the dorsal pterigiophores. Seven different color combinations were used to enable observers to identify dates of tagging through visual observation of fish on the spawning grounds.

TAG RECOVERY

Most tag recoveries (in-hand recoveries from dead fish and visual observation of live fish) were obtained from extensive foot and raft surveys of the spawning grounds. Spawning grounds were monitored by aerial surveys to determine the period of peak spawning. Each spawning area was surveyed once for tags, as closely as possible to the period of peak spawning. Additional tags were recovered from the sport fishery and from resident subsistence net catches. Some incidental loose tags were found in 1984 that had not been included in 1983 counts.

In addition, information on tagged fish migrating up the Newhalen River was recorded by FRI personnel during the Institute's enumeration program at RM 22.

Results

The 1983 harvest of Kvichak River sockeye salmon in the Naknek/Kvichak commercial fishery was estimated to be 16 352 189 fish and the escapement was estimated at 3 569 982 for a total run of 19 922 171 fish. The majority of the Kvichak River sockeye salmon run passes through the fishery in a short time, about 3 weeks, and fish that escape ascend the Kvichak River in the same time span. An average 6-day migration time from the Naknek/Kvichak commercial fishing district to the counting station at Igiugig was estimated from daily changes in sex ratios and proportions of net-marked fish, and from peaks and troughs in the escapement pattern at the counting station correlated with closures and catches in the commercial fishery. In addition, the correlation between catch and escapement was caculated for two periods (06/30–07/05 and 07/08–07/14) during which the fishery was continuously open. Lag times were varied from 3 to 8 days and the lag with the highest correlation coefficient for each period was selected. The lags selected were 6 days and 5 days, respectively. Therefore, daily catches were lagged 6 days and added to daily escapement counts to obtain the total estimated daily run (Fig. 2). The intense effort during fishery openings resulted in an escapement which consisted of three distinct pulses or segments of spawners. The first one included migrants through July 1, the second spanned escapements from July 2 through July 11, and the third from July 12 to the end of the migration.

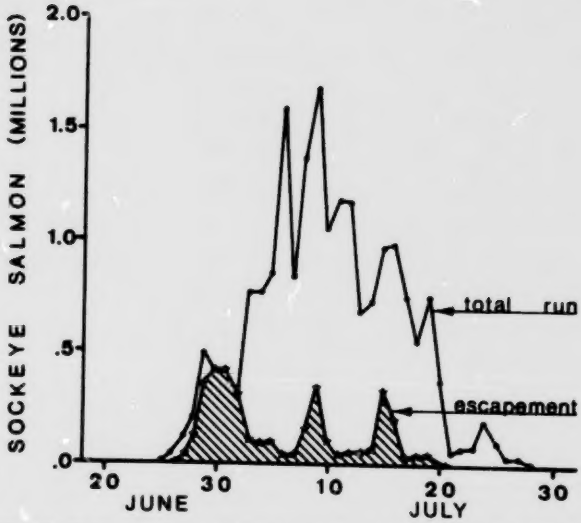

FIG. 2. Daily escapement of sockeye salmon into Iliamna Lake and estimated daily total run obtained by adding a day's escapement to catches made 6 days earlier, 1983.

Fish from the first pulse incurred a low exploitation rate (0.20) and provided 38.3% of the total escapement. Increased fishing effort on the second and third segments resulted in estimated exploitation rates of 0.88 and 0.89, respectively. The second and third segments contributed 37.0% and 24.7% to the escapement.

TAGGING

A total of 9 762 sockeye salmon was tagged from an estimated spawning escapement of 3 569 982 fish (Table 1). Seven different colors or color combinations were used, each of which was classified as representing a tagging (escapement) period (Table 1). Ratios of tagged to untagged fish ranged from 1:529 (period 1) to 1:244 (period 5) with an overall ratio of 1:366. Tagging periods 1 and 2 coincided with the first pulse of escapement, periods 3, 4, and 5 with the second, and 6 and 7 with the last pulse.

RECOVERIES

A total of 659 tags was recovered (in-hand recovery from dead fish and visual observation of live fish) on the spawning grounds. In addition, 73 tags were recovered from subsistence fisheries for an overall recovery rate of 7.5%. Subsistence recoveries were not included in the main analysis since fishing effort varied drastically during the season and between areas and since most of these fisheries were not ter-

TABLE 1. Schedule of adult sockeye salmon tagging by period at Igiugig, 1983.

Tag dates	Tag period	Tag color	Fish tagged	Tags 1 000 fish	Escapement count
6/28– 29	1	yellow/blue	984	1.89	520 518 (a)
6/30–7/1	2	yellow	1 958	2.32	845 274
7/ 2– 5	3	orange	1 992	3.32	599 160
7/ 6– 8	4	orange/white	935	3.82	244 938
7/ 9– 11	5	white	1 954	4.10	476 274
7/13– 15	6	blue/white	991	1.95	508 788
7/16– 19	7	blue	948	2.53	375 030 (b)
Totals			9 762		3 569 982

(a) Includes escapement of 3 132 fish prior to 6/28.

(b) Includes escapement of 30 750 fish from 7/20–23.

minal. Three assumptions were made in the subsequent analysis: (1) the shedding rate of tags did not differ between tagging periods, (2) tags from all periods were equally visible and distinguishable, and (3) the tagged fish were representative of the total spawning population. While the first assumption largely holds true, the second was not always correct for live fish since tag identification was governed by color or color combination, light conditions, and color perception of the various observers.

The average percent tag recovery by period was 6.7%, while the range extended from 3.6% (period 7) to 9.2% (period 4). The actual number of recoveries differed significantly from that expected if recovery rates were equal for all periods ($\chi^2 = 24.8$ with 6 df, $P < 0.0005$). There was no overall correlation between time of tagging and percent recovery, except that the rate of recovery from the final tagging period was about half of the average rate. More than half of the calculated chi-square value was due to the difference between observed and expected recoveries from period 7. If only periods 1 through 6 were considered, the actual number of recoveries by period did not differ significantly from that expected if recovery rates were equal ($\chi^2 = 10.3$ with 5 df, $0.05 < P < 0.1$).

The smaller than expected number of tag recoveries from the final escapement segment could have been due to sampling bias which would have occurred if a large and disproportionate number of fish from this group spawned in an area not surveyed or were not present on the spawning grounds during the surveys. These possibilities were rejected since all major spawning grounds were covered. Most recovery effort occurred on spawning grounds where there was little possibility of including fish destined to spawn in other areas. Recovery was conducted as closely as possible to the time of peak spawning to minimize immigration or emigration of spawners. Additional aerial surveys during the recovery periods showed few or no salmon schooled outside the spawning areas at the time they were surveyed for tags.

A more plausible cause of the low number of tag recoveries from the last tagging period was increased prespawning mortality of fish due to physiological stress. The majority of fish observed during the last tagging period exhibited well developed secondary sex characteristics associated with spawning. Males exhibited pronounced kypes and dorsal humps, females had extended abdomens, and both sexes usually displayed spawning coloration. Increased sexual maturity is coincident with degeneration and hypertrophy of most non-reproductive tissues and organs of sockeye salmon during the spawning migration. A study of almost sexually mature pink salmon in the Fraser and Thompson Rivers indicated that any delay in migration would probably result in pre-spawning mortality (J. R. McBride, Department of Fisheries and Oceans, West Vancouver, B.C., pers. comm.)

Many of the sockeye salmon in the final segment of the Kvichak River escapement appeared stressed from encounters with gillnets in the Naknek/Kvichak commercial fishing district. The fishery was continuously open for the 8 days preceeding the final tagging period, resulting in an estimated exploitation rate for the final run segment of 0.89. During the last tagging period (4 days), the proportion of net-marked fish ranged from 0.12 to 0.48.

We hypothesize that the combination of increased sexual maturity and stress from passage through the gauntlet of gillnets resulted in poor condition of migrants from the final run segment, thus a greater proportion of these fish than of early migrants was unable to complete migration to the spawning grounds.

A weighted recovery rate of tags for the final tagging period (7) was made by adjusting the actual recovery rate to the average rate of tag recovery from the first six tagging periods by:

$$r_7^* = 1/6 \; (\sum_{i=1}^{6} \frac{r_i}{T_i}) \bullet T_7$$

where r_7^* is the adjusted tag recovery from period 7, r_i is actual recovery of tags from period i, and T_i is the number of fish tagged during period i.

The number of recoveries from any period was dependent on the number of fish tagged. In addition, a different proportion of the escapement was tagged during each period, therefore, it was necessary to adjust recoveries to make them directly comparable to the period escapement size. This was accomplished by weighting the number of fish tagged during each tagging period to the average rate of tagging for all periods. Thus, the adjusted tag recoveries for each period were obtained by:

$$r_i^* = r_i \bullet 1/7 \; (\sum_{i=1}^{7} \frac{T_i}{N_i}) \bullet \frac{N_i}{T_i}$$

or

$$r_i^* = r_i \bullet (0.0028) \bullet \frac{N_i}{T_i}$$

TABLE 2. Actual tag recoveries and recoveries adjusted for unequal tagging and recovery rates from the 1983 Kvichak River sockeye salmon escapement.

Recoveries	Tagging period							
	1	2	3	4	5	6	7	T
Actual	67	123	152	86	136	62	34	659
Adjusted	100.9	151.2	130.2	64.1	93.7	90.6	76.6	707.3

where N_i is the total escapement in period i and $r_i^* = r_i$ adjusted for unequal tagging rates between periods (Table 2). The following analysis is based on the adjusted recoveries.

The migratory structure of sockeye salmon populations has been shown to differ between geographic areas, between habitat types (river vs beach spawners), and between early and late spawning groups. Therefore, we analyzed the recoveries from three different viewpoints, (1) the geographic distribution of recoveries and the distributions of recoveries based on (2) types of spawning grounds and on (3) time of spawning, all related to time of passage at the tagging/counting station at Igiugig.

When recoveries were arranged within nine geographic areas (Fig. 3) and by the seven tagging periods, there were recoveries from every tagging period in every area. The central 80% of migration spanned six tagging periods in all cases except for one where five tagging periods were represented (Fig. 4).

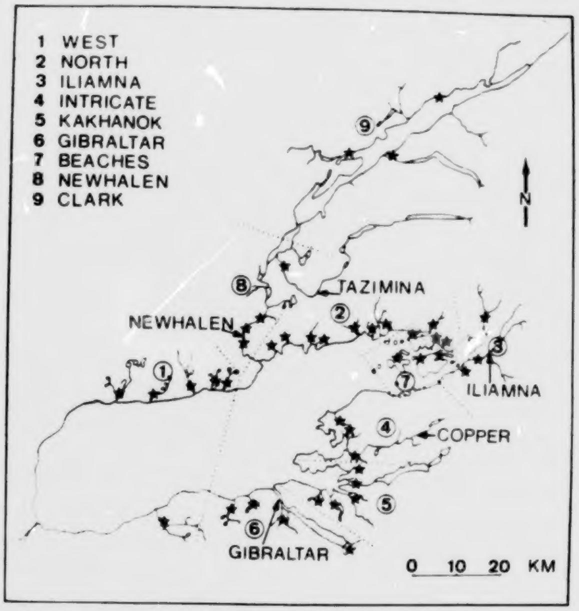

FIG. 3. Geographic boundaries of the nine spawning areas in Iliamna Lake and Lake Clark. River spawning areas are labeled, other water-courses are streams, and the stars represent the major spawning grounds from which recoveries were made, 1983.

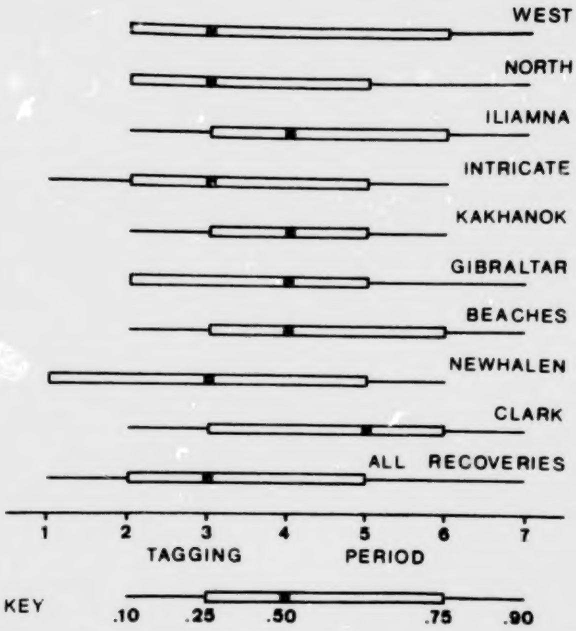

FIG. 4. Migratory timing estimated from the proportion of recoveries by tagging period for sockeye salmon in each geographic area in the Kvichak River watershed, 1983.

Recoveries were reorganized by type of spawning habitat. The majority of spawners utilize four types of spawning areas: small streams and creeks, large rivers, mainland and island beaches, and spring-fed ponds. The last type was excluded because of very low escapements in 1983. Fish adapted to such diverse spawning habitats might exhibit specific migratory timing. Yet, each of the seven tagging (escapement) periods was represented on each of the three types of spawning habitats. The central 80% of migration spanned six tagging periods, and the central 50% spanned periods 2 through 5 in all habitat types (Fig. 5).

The spawning of Kvichak River sockeye salmon stocks spans 4 months. Early spawning was completed more than a month before late spawning commenced. The dates of peak spawning vary little between years in a given area.

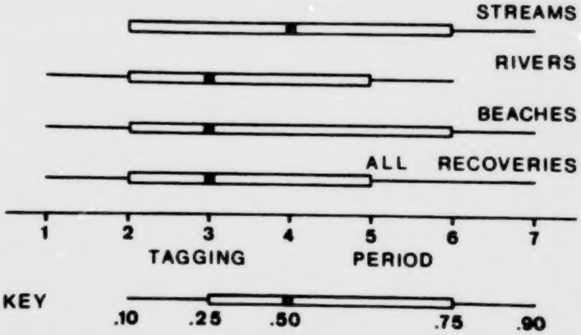

FIG. 5. Migratory timing estimated from the proportion of recoveries by tagging period for sockeye salmon in each type of spawning habitat in the Kvichak River watershed, 1983.

Recoveries from the early, middle, and late spawning components were compared to determine if a correlation existed between time of ascent and time of spawning in the Kvichak River watershed. The three components were defined by time of peak spawning: early (peak spawning prior to August 10); middle (peak spawning between August 11 and September 20); and late (peak spawning after September 20). Every tagging period was represented in the recoveries from each component, and the central 80% of migration spanned at least six tagging periods (Fig. 6). The central 50% of migration began slightly later for early spawners (periods 3-6) than for middle (periods 2-5) and late (periods 2-6) spawners.

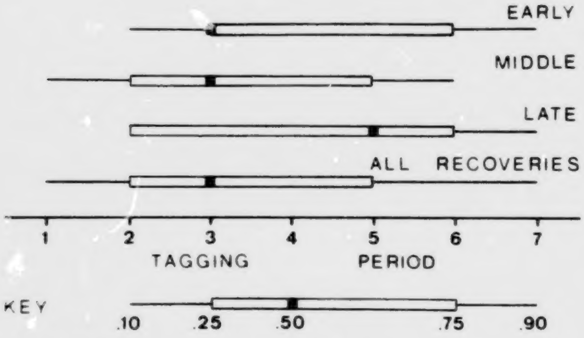

FIG. 6. Migratory timing of the early, middle, and late spawning components of the 1983 Kvichak River sockeye salmon spawning escapement, estimated from recoveries from seven tagging periods.

Another method used to compare the migratory structure of the various run components was the estimated mean of migratory time density ($\bar{t}$) and its variance (s^2). In this case the s^2 is a minimum variance estimate since the variances of the adjustments to tag recovery rates are not included. This process quantifies the relative abundance of a migratory group as a function of time (Mundy 1979, 1982):

$$f(t_i) = r_i^* / \sum_{i=1}^{7} r_i$$

$$\bar{t} = \sum_{i=1}^{7} i \bullet f_i$$

$$s^2 = \sum_{i=1}^{7} (i - \bar{t})^2 \bullet f_i$$

where $f(t_i)$ is a discrete time density function.

The homogeneity of the calculated variances was tested with Bartlett's test (Bartlett 1937) with an adjustment to more accurately approximate the chi-square distribution (Zarr 1974). There were no significant differences in variances of mean timing in the nine geographic areas ($B_C = 2.425$ with 8 df, $0.95 < P < 0.975$) or the three spawning habitat types ($B_C = 1.330$ with 2 df, $0.90 < P < 0.95$), or the early, middle, and late spawning components ($B_C = 0.54$ with 2 df, $0.95 < P < 0.975$). Since the variance of the migratory time density function was essentially the same in the different geographic areas, different habitat types, and even in the early, middle, and late spawning components, it appears to be an important aspect of overall fitness.

Since there were no significant differences in variances, the equality of means of migratory time density in each grouping (Table 3) was tested with ANOVA. Although the Newhalen area appeared to have an early mean migratory date and the Clark area a late mean, there were no significant differences in the mean dates of migration to the different geographic areas ($F = .00066$ with 8698 df, $P >> 0.75$). There were no significant differences in the mean migratory date of spawners in the different habitat types ($F = 0.00128$ with 2704 df, $P >> 0.75$) or between the early, middle, and late spawners ($F = 0.0084$ with 2704 df, $P >> 0.75$).

TABLE 3. Estimated date of mean of migratory time density and variance for various escapement components of the 1983 Kvichak River sockeye spawning escapement.

Escapement component	Sample size	$\bar{t}$	Estimated date	s^2
	Geographic area components			
West	56	4.02	07/06	4.18
North	40	3.78	07/04	3.19
Iliamna	105	4.12	07/06	3.31
Intricate	79	3.63	07/02	3.46
Kakhanok	34	4.13	07/06	2.63
Gibraltar	48	3.97	07/05	3.67
Beaches	35	4.16	07/06	3.79
Newhalen	287	3.21	07/02	3.88
Clark	23	4.59	07/08	3.81
	Spawning bed type			
Stream	178	3.99	07/05	3.47
River	480	3.54	07/03	3.86
Beach	49	3.86	07/05	4.35
	Period of spawning			
Early	38	4.21	07/06	3.85
Middle	646	3.61	07/03	3.79
Late	23	4.59	07/08	3.81
	Combined recoveries			
Total	707	3.67	07/03	3.84

MIGRATORY STRUCTURE WITHIN A SPAWNING AREA

In individual spawning systems, recoveries were made both from schooling/spawning and spent fish. There were sufficient recoveries in three rivers to compare the migratory distribution of unspawned or spawning fish with that of spent fish (Fig. 7). In each river, the distribution of recoveries indicated that the spent fish had migrated slightly earlier than the unspent fish. However, the migratory timing indicated by recoveries from each group overlapped considerably. Thus, in all three rivers, there were schooling/spawning fish bearing tags from periods 1 or 2 together with spent fish bearing tags from period 4 or later. This pattern was indicated for most spawning grounds however in those areas with few recoveries it was not possible to determine if a lack of overlap was due to a real separation or to a small sample size.

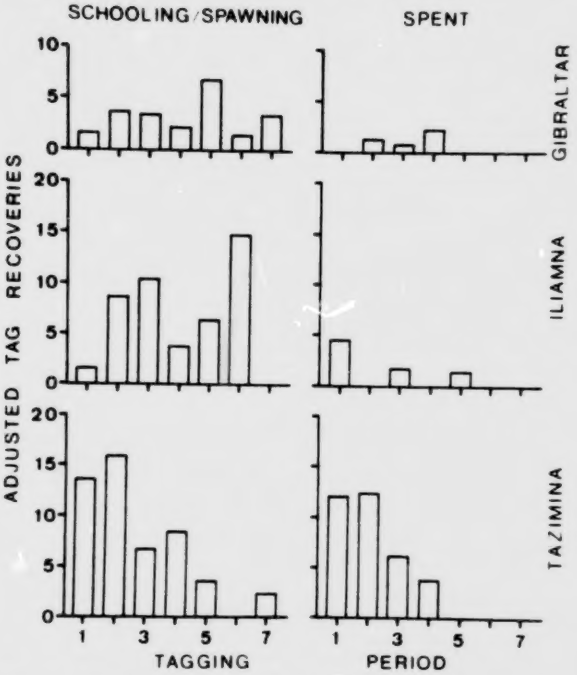

FIG. 7. Comparison of recoveries from schooling/spawning sockeye salmon and spent fish determined at a single survey during estimated peak spawning time in three rivers in the Kvichak River drainage, 1983.

The extent of the intermingling of fish from different escapement periods was indicated by tags sighted at the Newhalen River counting site. Migration up the Newhalen River peaked in mid-July and a second, smaller peak occurred at the end of July. The duration of migration of fish from the 2–4 day tagging periods was greatly protracted. Migration of fish from each of the first 3 escapement periods (indicated by tag sightings) spanned more than 3 weeks and overlapped by a minimum of 16 days. Increased turbidity of the river after mid-July resulted in decreased tag sightings, and no tags were sighted from periods 6 and 7.

Recoveries from actively spawning fish were arranged by tagging (escapement) period to obtain conservative estimates of the dates of earliest and latest spawning (Fig. 8). The minimum period of active spawning of fish from a given tagging period ranged from 30 to 70 days. Some fish from each escapement period began spawning almost immediately while others in each period waited 1 or 2 months or longer before spawning. There was a great degree of overlap in timespan of active spawning among fish tagged during each of the seven tagging periods. In other words, some of the early migrants had the opportunity to mate with the late migrants, which indicated the potential for panmictic spawning populations.

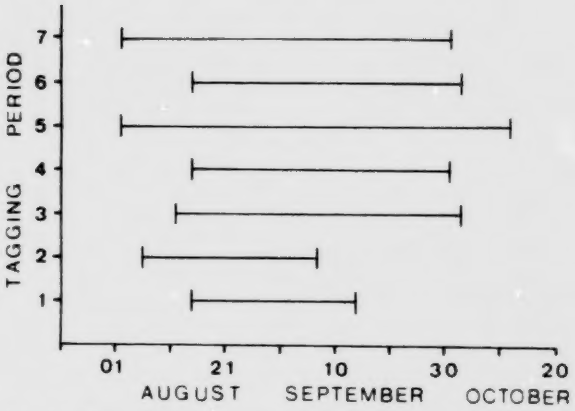

FIG. 8. Conservative estimates of the timespan of active spawning determined from recoveries of earliest and latest actively spawning sockeye salmon tagged during seven tagging (escapement) periods in the Kvichak River, 1983.

Conservative estimates of minimum and maximum lifespans were obtained from observations of the first dead (spawned out) and the last live tagged fish from each tagging period (Fig. 9). The estimated lifespan ranged from less than 20 days to more than 80 days. There were live fish from every tagging period present simultaneously on the spawning grounds for a minimum of 20 days. Although individual fish were not studied, it appeared that crossings of all segments of the escapement were possible and probably happened, although this is still based on speculation.

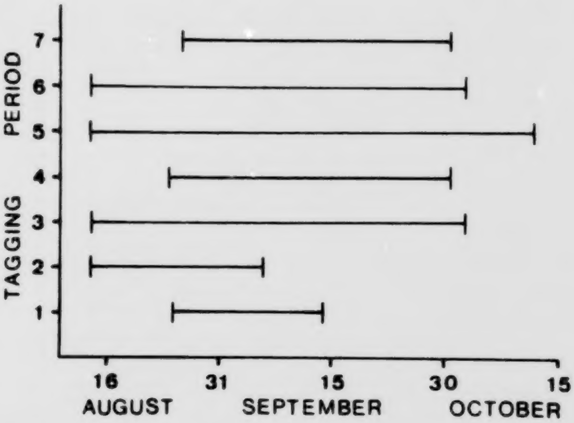

FIG. 9. Conservative estimates of minimum and maximum lifespan determined from observations of first dead and last live sockeye salmon tagged during seven tagging (escapement) periods in the Kvichak River, 1983.

Discussion

Most of the Kvichak River sockeye salmon stocks had migratory timing patterns that did not differ significantly from the timing of the entire escapement. In 1983, the majority of migrants passed the Igiugig counting station during a 21-day period. Thompson (1951) examined the duration of ascent of sockeye salmon as a function of latitude and established a declining window (timespan) with higher latitude within which the fish must return in order to reproduce successfully. This boundary apparently is not set by conditions in the freshwater environment since spawning extends over a 4-month period. The compression of the migration of Kvichak River stocks and stocks destined for other rivers in Bristol Bay appears to be caused by oceanic conditions. Bristol Bay sockeye salmon return from the feeding grounds in the ocean, principally at a total age or 4, 5, or 6 years. In their final year of life, the majority of the salmon begin congregating south of the Aleutian Islands in May. Some migrants pass around Attu, the last island in the Aleutian Island chain, some 1600 km from Bristol Bay. Other sockeye salmon migrate through channels between the islands. Topographical effects and upwelling cause vertical mixing of the water in the channels between the islands. This creates a high salinity, low temperature water layer in the passes which blocks salmon migration. The barrier disappears in June and July due to changing wind, tide, and current patterns which push water northward through the passes. Migrants follow a mixed water mass and salinity gradients into Bristol Bay (Fujii 1975). However, after entering the nursery areas (in this case, Iliamna Lake and Lake Clark), the window within which successful spawning can occur expands to about four months. There appears to be ample opportunity for temporal segregation of the various components of the escapement past Igiugig.

When the migratory distribution of spawners in Iliamna Lake was compared with that in the Newhalen River-Lake Clark complex there were differences. Overall, the latter had a higher proportion of early migrants, but Lake Clark by itself had a higher proportion of late migrants than did Iliamna Lake. However, the estimated means of migratory time density were not significantly different. The calculated variances also were not significantly different from each other and were of the same magnitude as that of the entire escapement. Each spawning component received fish from every segment of the total Kvichak River escapement. This holds true regardless of whether one considers geographic locations, type of spawning habitats, or the early, middle, or late spawning components. Another tagging experiment in the Egegik River mouth in 1947 produced similar results (Mathisen 1969). The escapement entering both Iliamna Lake and Lake Becharof each day is comprised of a mixed group of spawners which acts as a buffer to secure an escapement to all spawning grounds. This is especially important if some segments of the run experience a differentially high exploitation rate, as was clearly observed in 1983 when an exploitation rate of 80% or greater reduced the Kvichak River escapement to a trickle when the fishery was operating and resulted in a trimodal escapement curve. In other instances, high water level can block migration as was observed in the Newhalen River in 1980 where perhaps as many as 5 million spawners failed to navigate the river (P. H. Poe, University of Alaska, Juneau, Ak. pers. comm.). In spite of the low effective escapement, no stream was void of spawners in Lake Clark. It seems plausible that early migrants have a higher potential of successfully navigating the rapids than do middle period migrants. This would be particularly important if the block occurred midway through the migration or later. Since water levels generally drop in the Newhalen River in late summer, late migrants might also have greater success at navigating the rapids than middle migrants. The relatively high proportion of late migrants among the Lake Clark spawners might also be due to the physical characteristics of the system. Lake Clark, especially the upper portion where the majority of spawning occurs, is characterized by a high sediment load from glacial tributaries. Personal observation of glacial and nonglacial salmon systems in Southeast Alaska indicates that stocks in glacial systems tend to have late migrations. Late migration could result in deposition of eggs after the water level drops in the fall and the water becomes clearer, reducing the potential for stranding or oxygen starvation due to silting.

The partial temporal segregation of migrants destined for Iliamna Lake and for Newhalen River–Lake Clark spawning grounds permit some management alternatives. It is now not only possible to seek a harvest rate which will result in a preassigned escapement goal to the Kvichak River system, but it is also possible to influence the distribution of the spawners between the two major systems.

Perhaps the most important finding of this study was the relatively constant magnitude of the variances of the means of migratory time density exhibited by all major spawning groups. Even those races with the earliest and latest periods of peak spawning had substantial proportions of migrants from all segments of the escapement.

Secondly, extensive mixing of migrants from different temporal run segments on the individual spawning grounds suggested almost panmictic spawning populations. In some areas, the first arriving sockeye salmon did not spawn until some of the later migrants had spawned and died.

Studies of contemporary population biology which include population genetics and evolutionary genetics have quantified some simple principles concerning reproductive success. In the case of salmon management, the idea of genetic management is surfacing regularly as a further extension of classical population management. Emlen (1984) defined fitness for a given genotype as the average number of offspring produced. For each population there exists a probability distribution of fitness with a mean value $\bar{W}$ and a variance V_w. Conservative management then dictates that mean and variance (probability distribution of fitness) should be maintained in successive generations to act as a buffer in changing environments (Kapusciniski 1984). The mean of migratory time density and its variance appear to be important aspects of fitness. If so, it follows that a successful spawning population should include elements of the entire run in proportion to their probability curve based on historical abundance. Management practices imposed on the pink salmon fishery in Southeast Alaska following the *White Act* of 1924 specified an exploitation rate of 50%. The fishery was allowed to harvest its 50% share from the first part of the run leaving the last half for escapement. The end result was later and later peak spawning time and progressively lower and lower survival of the progeny (Alexandersdottir and Mathisen 1982).

Continual removal of specific temporal segments over many years can result in reduced fitness and survival of salmon stocks. However, our study indicated that the broad span of migratory timing of specific stocks can buffer the effects of the removal of temporal components of a migration in a single year. This paper focused on one aspect of fitness by studying in detail the migratory distributions and the mean and variance of migratory time density functions for sockeye salmon spawning populations in the Kvichak River system of Bristol Bay. Although there were some variations due to sampling, all components, regardless of geographic location, type of spawning habitat, or period of peak spawning possessed about the same variance. Basically this could be interpeted as a buffering mechanism against extinction.

Acknowledgements

Thanks are expressed in a collective manner to all persons who contributed to the success of this study, both through assistance with field work and through support during the analysis and writing. We especially wish to acknowledge the effort expended by Mr. Pat H. Poe, Project Leader of the FRI field crew in 1983, without whom this study would not have been possible.

This study is part of a larger tagging experiment conducted in the Kvichak River watershed with financial support from the University of Alaska, Juneau and from the Fisheries Rehabilitation Enhancement and Development Division and the Commecial Fisheries Division of the Alaska Department of Fish and Game. The latter agency also supplied assistance in the field through the efforts of their employees during the tagging operation and the use of their facilities at Igiugig. Fisheries Research Institute (FRI, University of Washington) personnel participated in recovery efforts in addition to operating the Newhalen River counting station. Recovery efforts were dependent upon the use of their facilities at Roadhouse and at Porcupine Island. Additional financial support was given by the salmon processors of Bristol Bay through the Pacific Seafood Processors Association.

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The Adaptive Significance of Age and Size at Maturity in Female Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

HEALEY, M. C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*), p. 110–117. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

When both the freshwater and marine components of their life history are taken into account, female sockeye mature at 14 different age categories among five different total ages. Within an age class, mean length among populations commonly varies 9 cm. Fecundity and egg size are increasing functions of female size but fecundity varies less with size in sockeye salmon than is common among fishes. Fecundity adjusted for size varies 30–50% among populations. The traditional explanation for this variation is that it is caused by environmental fluctuations. Implicit in this explanation is the assumption of a critical minimum size for smolting and maturation. In many instances the notion that smolting and maturation are triggered by the achievement of a critical minimum size must be rejected. A life history model driven by age specific patterns of natality and mortality also failed to account for variation among populations. Variation within populations may be explained by a game theory model driven by competition for nest sites and differential survival of eggs in gravel of variable porosity.

Résumé

HEALEY, M. C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*), p. 110–117. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Compte tenu des stades vitaux passés en eau douce et en eau salée, les saumons nerkas femelles atteignent la maturité à 14 catégories d'âge réparties en 5 catégories d'âge total. Au sein d'une classe d'âge, la longueur moyenne entre les populations varie en général de 9 cm. La fécondité et la taille des oeufs sont en proportion directe avec la taille de la femelle quoique la fécondité varie moins avec la taille chez le saumon nerka que chez les poissons en général. La fécondité corrigée en fonction de la taille varie de 30 à 50 % parmi les populations, une variation communément attribuée aux fluctuations environnementales. Par induction, on suppose l'existence d'une taille minimum critique pour la smoltification et la maturation. Dans plusieurs cas, on doit rejeter le concept que la smoltification et la maturation sont déclenchées par une taille minimum critique. Un modèle du cycle vital axé sur les régimes de natalité et de mortalité selon l'âge n'a pas non plus justifié la variation entre les populations. La variation au sein des populations peut être expliquée par un modèle de la théorie des jeux axé sur la compétition pour les frayères et la survie différentielle des oeufs dans le gravier à porosité variable.

Sockeye salmon (*Oncorhynchus nerka*) are distributed from northern Hokkaido north to the Anadyr River on the Asian coast and from the Sacramento River north to Kotzebue sound and possibly into the Canadian Arctic on the North American Coast (Hart 1973). Throughout the species range, populations show considerable variation in parameters of reproduction (Healey 1986).

If we assume that each population of sockeye is adapted to the particular environment within which it lives and reproduces, then we must also accept that evolution has operated, and is still operating, so as to increase the fitness (i.e. contribution of genetic material to future generations) of individuals within each population. Even though it may never get there, we can think of the population as constantly moving toward some maximum fitness. Thus, the variation in parameters of reproduction among populations reflects adaptations to maximize fitness in local environments. From an evolutionary perspective, therefore, it is appropriate to ask several questions about the reproductive tactics of female sockeye, such as:

1) What age and size at maturity will maximize female fitness?
2) What number and size of eggs will maximize female fitness?
3) What allocation of surplus food energy among competing processes of somatic growth, egg production, spawning, and survival activities will maximize female fitness?

In this paper I shall first describe the range of reproductive tactics adopted by female sockeye in terms of variation in age and size at maturity, fecundity and egg size. Then

I shall attempt to account for inter- and intra-population variation in tactics in terms of predictions from life history theory, placing particular emphasis on age and size at maturity within and among populations.

Age and Size at Maturity, Fecundity, and Egg Size of Sockeye

The data that I used on age composition of females in spawning populations come from several sources. Data for the Ozernaia River in Kamchatka are from Hanamura (1966) and for Bristol Bay stocks are from Yuen et al. (1981). Data for southeastern Alaska stocks came from a survey of many streams reported by McGregor et al. (1984). Sample sizes for some of the populations McGregor et al. (1984) surveyed were quite small. I used only those populations for which the sample size was greater than 200. Data on British Columbia spawning runs came from Foskett (1952, 1953, 1954, 1955), Foskett and Jenkinson (1956), and Killick and Clemens (1963). Measurements of average female size came from the same sources with the addition of data for the Kuskokwim, Cook Inlet and Prince William Sound areas of Alaska from Huttunen (1985), Roberson et al. (1983), and Schroeder (1984, 1985). Most of the data on mean age and size from these sources refer to mixtures of spawning populations, so that the real variation among individual population means may be even greater than that suggested by these data.

Sockeye mature from their third to their eighth year of life (Healey 1986). Female sockeye, however, which are the focus of this paper, have not been recorded older than in their seventh year (Fig. 1). If both freshwater and ocean age are taken into account, then sockeye mature at 22 different age categories (Healey 1986). Female sockeye, however, mature at only 14 different combinations of freshwater and ocean age (Fig. 1). Four of these age categories (1.2, 1.3, 2.2, and 2.3 in the European system: freshwater annuli • saltwater annuli) are present in most populations and generally make up the dominant age classes of females in some combination (Fig. 1). Five other age categories (1.1, 0.3, 1.4, 3.2, and 3.3), although they are relatively common in occurrence among populations, and may contribute several percent to the female spawning population, are never abundant in any population (Fig. 1). Five age categories (0.2, 2.1, 0.4, 3.1, 2.4) occur as rare variants in some populations (Fig. 1). Males have been reported from eight other age categories, but not females.

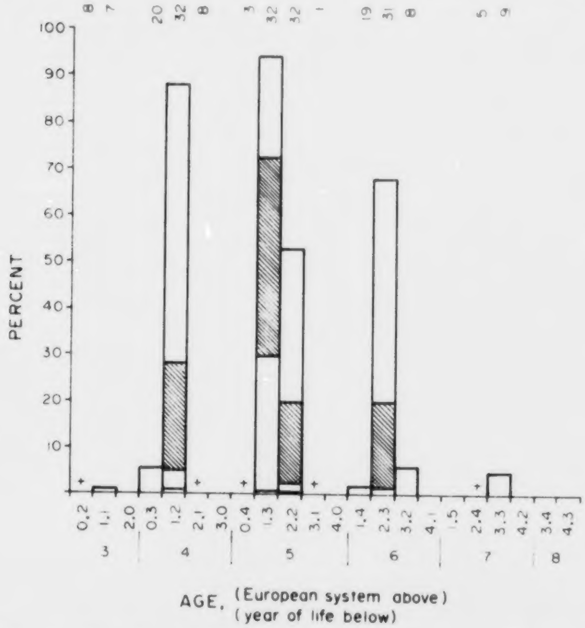

FIG. 1. Contribution of different female ages to 32 spawning populations of sockeye. Bars represent the range in percent contribution among populations. Shaded areas of the longer bars represent percentages within which half the populations fall. (+) indicates that the age category was observed in small numbers. The numbers across the top of the figure show the number of populations among those surveyed in which the age category was reported. See text for literature sources.

Within and between population variation in age composition of females is further demonstrated by individual populations in Bristol Bay and British Columbia (Table 1). The age composition of each of these populations is based on a large sample and is the mean of a number of years of observation, so that each should be relatively free from year to year variation and problems of small sample size. The number of age categories present in each population varies from 5 to 10 and the number of different total ages from 3 to 5 (over the range of ages 3 to 7 years). In some cases several age categories contribute strongly to the spawning run, such as the Kvichak and Naknek Rivers in Bristol Bay in which 4 different age categories representing 3 different total ages are about equally abundant. In other cases a single age class dominates, such as in the Fraser River, British Columbia, in which 88% of the fish are aged 1.2 (Table 1).

Several conclusions are possible from these data. First, female sockeye typically mature at several total ages, and at even more combinations of fresh water and marine age. Not all these age categories are equally succesful life history tactics, however, at least if abundance is considered to be a measure of success. Second, although northern populations tend to mature at an older total age than southern populations, mainly because they spend longer in fresh water, this is not a universal rule, and latitude appears to be only weakly correlated with age at maturity. Populations that spawn in geographical proximity can differ greatly in the contribution of different age categories to the spawning population. Third, differences in age structure among populations result mainly from variation in the contribution of a few age categories that are abundant in all populations, rather than variation within the whole suite of potential age categories. Finally, variation in age is not concentrated in either the freshwater or marine phase, both phases show about the same absolute variation in age among populations.

Just as mean age at maturity varies considerably within and among populations so does mean size within an age class vary among populations. For 51 sockeye populations in Alaska the mean length (mid-eye to fork of tail) of females aged 1.2 ranged from 44.8 to 53.6 cm and of females aged 1.3 ranged from 50.8 to 59.5 cm (Fig. 2). This broad range in average size among mature females from different populations (14.7 cm difference between largest and smallest) for the commonest age classes suggests that variation in age among populations is not a mechanism to ensure that mature fish are of a particular size. Nor is there a correlation bet-

TABLE 1. Average percent age composition of sockeye females from spawning runs to ten Bristol Bay rivers and five British Columbia rivers. (+) indicates that the age category contributes <0.5% to run. Data are from Yuen et al. (1981), Foskett (1952–1955), and Foskett and Jenkinson (1956).

River	Age: Year of life/European designation														Mean age (years)		
	3		4			5				6			7			Fresh	
system	0.2	1.1	0.3	1.2	2.1	0.4	1.3	2.2	3.1	1.4	2.3	3.2	2.4	3.3	Total	water	Marine
Alaska																	
Kvichak	+		+	25	+		19	38		+	18	+			4.94	2.56	2.38
Egegik			+	11	+		13	42	+		29	4	+	+	5.18	2.77	2.41
Naknek				22			31	26		+	20	+	+	+	4.94	2.44	2.50
Ugashik	+		+	18	+		26	45			10				4.89	2.54	2.34
Branch		1		60	+		27	10			2	+			4.40	2.12	2.28
Wood	+	+	+	55	+	+	34	7		+	4			+	4.50	2.11	2.39
Igushik			+	20		+	60	11		+	8		+		4.85	2.18	2.67
Nuyakuk	+		7	20			69	2		+	2				4.75	1.97	2.78
Snake				67			24	7		+	2				4.35	2.09	2.26
Togiak	+	+	+	38			47	7		+	6				4.61	2.11	2.50
B.C.																	
Nass	+		2	23	+		16	53		+	5			+	4.76	2.55	2.21
Skeena			+	47			45	5			3			+	4.56	2.08	2.48
Rivers Inlet			+	37			62	+		+	+				4.60	1.99	2.61
Smith Inlet			+	29			71	+		+	+				4.72	2.00	2.72
Fraser		+	+	88			9	2							4.08	2.01	2.07

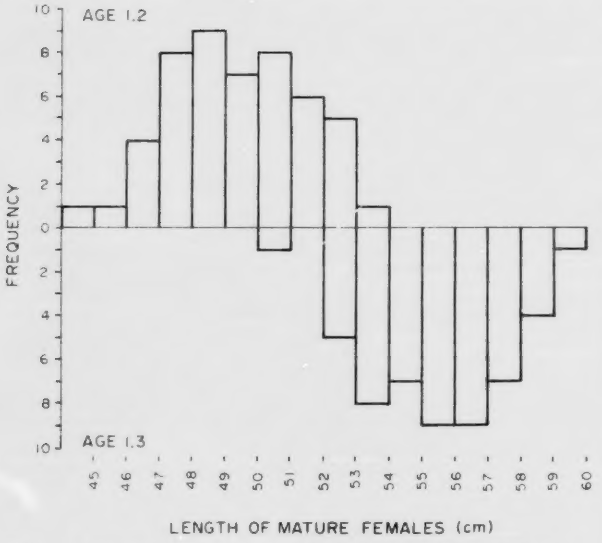

FIG. 2. Frequency histograms of length (cm, mid-eye to fork of tail) for 51 Alaskan populations of sockeye at ages 1.2 and 1.3. Mean length at age was taken from Alaskan Dep. of Fish and Game technical data reports (see text).

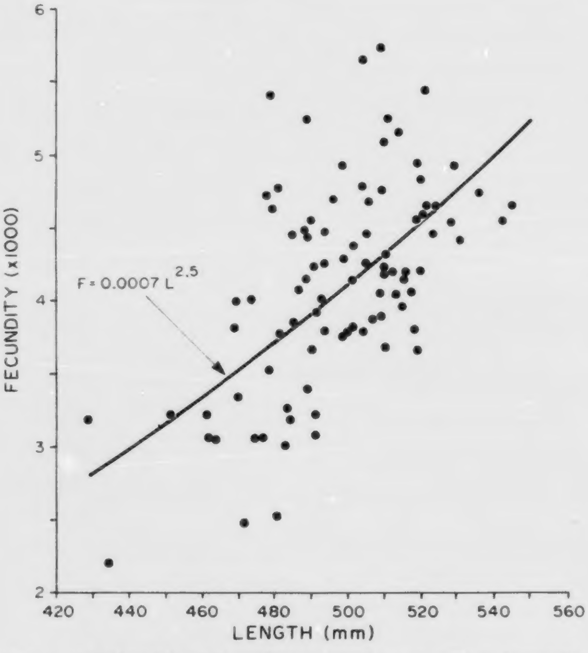

FIG. 3. Relationship of fecundity to length (post-orbit to hypural) for Iskut River commercial catch of sockeye. Data were a personal communication from Dr. C. Wood, Dep. Fisheries and Oceans, Nanaimo, B.C.

ween mean size at age and mean age in the population, as would be expected if size and maturity schedule were strongly linked within populations. Any model that attempts to explain age and size at maturity in sockeye must be able to account for the occurrence of old and young spawners, and of large and small fish, within and among populations.

Whatever the conditions that determine the age and size at which sockeye females mature, they will have inevitable consequences for the number of eggs each female produces. Female sockeye produce between about 2000 and 6000 eggs depending on their size and the population to which they belong (Foerster 1968). In general, fecundity increases with the size of the female both within and between populations. The basic features of the relationship between fecundity and size are demonstrated by a plot of fecundity on post-orbit/hypural length for Iskut River sockeye sampled from the commercial catch (Fig. 3) (I am indebted to Dr. C. Wood, Canada Department of Fisheries and Oceans, Nanaimo, for permission to use these data). These features are that only a small percentage of the variation in fecundity is attributable to variation in length and that the slope of the regression of fecundity on length is shallow. For the Iskut data the regression of $\log_e$ fecundity on $\log_e$ length explained only about 37% of the variation in fecundity and the slope of the regression was 2.5. Ordinarily, one would expect fecundity to be directly proportional to weight, so that the slope of the regression of log fecundity on log length should be about 3.0 or slightly greater (Bagenal 1967). Manzer and Miki (1986) found that the slope of the regression of log fecundity on log length for 14 British Columbia sockeye stocks ranged from − 2.99 to + 2.91 with 12 of the 14 having slopes less than 2.0. The variation in fecundity explained by variation in length was also low in Manzer and Miki's study, ranging from 1% to 82% but with 10 of the 14 relationships explaining less than 50%.

Despite the high variablility in fecundity, it is still possible to detect significant differences in both the slope and intercept of the fecundity on length regression among populations. Foerster (1968) reported fecundity data for a number of populations that suggested differences on the order of 1 000–1 200 eggs between females of the same size in different populations. Manzer and Miki (1986) observed statistically significant differences in fecundity at 447 mm post-orbit/hypural length among sockeye from different populations in coastal British Columbia, the maximum differences being 1 193 eggs among fish aged 1.2 and 2 293 eggs among fish aged 1.3.

Clearly, there is a lot of variation in fecundity to explain, both within and between populations. The fact that populations differ in fecundity at the same body size suggests that each population may have adopted a different solution to the poblem of allocating surplus energy among competing biological processes (question 3 above). The high variation in fecundity among individuals of the same size within a population further suggests either that individuals experience quite different feeding histories during marine life or that individuals within a population may have different programs for the allocation of surplus energy.

The variation in fecundity between and within populations may reflect an important trade-off between egg size and egg number. Egg size increases with fish size in sockeye (Bilton and Jenkinson 1966), so that the low slope of the fecundity on length relationship may, in part, be due to the fact that the larger fish are producing larger and, therefore fewer, eggs per unit of body size. Egg size has not been investigated in detail among populations. It may be the case, however, that populations with higher average fecundity have smaller egg size, and also that individuals with higher fecundity for their size have smaller eggs. Such relationships would merely increase the complexity of the problem, however, since one must then ask not only what is the appropriate egg number to maximize fitness, but also what is the appropriate egg size.

Explanations for Variation in Reproductive Tactics

I have shown that there is considerable variation in body size, age, fecundity, and egg size among mature sockeye both within and between populations. These characters do not vary independently, rather, they tend to group in sets that comprise recognizable strategies. Size and age are obviously linked, but larger, older spawners also tend to produce somewhat more eggs and larger eggs. Smaller, younger spawners produce fewer (but not proportionately fewer) smaller eggs.

The traditional explanation for this variation in parameters of reproduction is that it is caused by environmental fluctuations. Under this hypothesis the fundamental pattern for sockeye is to spend a year in fresh water before going to sea, and to mature after 2 years at sea (i.e at age 1.2). Other periods of fresh water and marine residence occur as a consequence of precocial or delayed development caused by conditions that favour or inhibit growth in one or the other environment (Foerster 1968).

This explanation seems to hinge on the assumption of threshold sizes for smolting and maturation. There may well be minimum sizes for successful smolting and for maturation. Sockeye do not necessarily smolt as soon as possible after reaching a minimum smolt size, however, nor do they mature as soon as possible after reaching a minimum adult size. Analysis of smolt size at age reveals numerous populations in which two or three year old smolts were large enough to smolts as yearlings or two year olds (Randall et al. 1987). Similarly, the large range of sizes among the most common age groups of mature sockeye and the lack of a correlation between the mean age of spawners and the size of age 1.2 or 1.3 females are inconsistent with the idea that maturation takes place as soon as possible after the fish reach a threshold size. Even if one assumes a unique threshold size for each population, the range of ages and sizes of females present in most populations is, in my view, too great to be accounted for wholly by environmental variation. To assume a unique threshold size of maturation for each population further implies genetic adaptation of both fresh water and marine age to local conditions.

Other models to explain size and age at maturity also imply local genetic adaptation to maximize fitness. These are models developed in the field of life history theory. They fall generally into two classes, optimization models (Stearns 1976, 1977; Stearns and Crandall 1984), which assume no density dependent or frequency dependent selection within the population, and game theory models (Maynard Smith 1982), which assume frequency dependent selection.

Schaffer and Elson (1975), Leggett and Carscadden (1978), Healey and Heard (1984), and Healey (1986) used optimization models to explore aspects of age and size at maturity among anadromous fishes. The approach taken by Healey and Heard (1984) was to compare parameters of reproduction in chinook salmon (*O. tshawytscha*) with predictions from a model proposed by Bell (1980). A similar approach is appropriate for sockeye, and here I expand on an analysis first described in Healey (1986).

Bell's (1980) model is built on the observation that for ectothermic animals with indeterminate growth, like fishes, both size and fecundity increase with age, but that the rate of increase declines with increasing age. If one assumes that the population structure is driven by the age-specific patterns of natality and mortality, then the optimum age at which to mature is the age at which the instantaneous rate of increase in fecundity is equal to the instantaneous rate of natural mortality of animals in the mature age classes. An animal that matures at a younger age is losing reproductive opportunity (and lowering its fitness) because its rate of increase in egg production is greater than its probability of dying before the next spawning season. An animal that matures at an older age is losing reproductive opportunity for the opposite reason. Consequently, for sockeye, the optimum age at which to mature is the age at which a line having slope equal to the instantaneous rate of natural ocean mortality is tangent to the curve of instantaneous increase in egg production with age.

Data for seven sockeye populations are available to test this prediction. Two of the populations may be further subdivided into fish which went to sea at different ages, giving a total of nine fecundity on age curves (Fig. 4). Estimates of natural mortality of sockeye in the ocean, as reviewed by Ricker (1976), range from 0.14 to 0.24 with a mean of 0.18. Thus, in Fig. 4, lines of slope 0.18 are plotted for comparison with the fecundity curves.

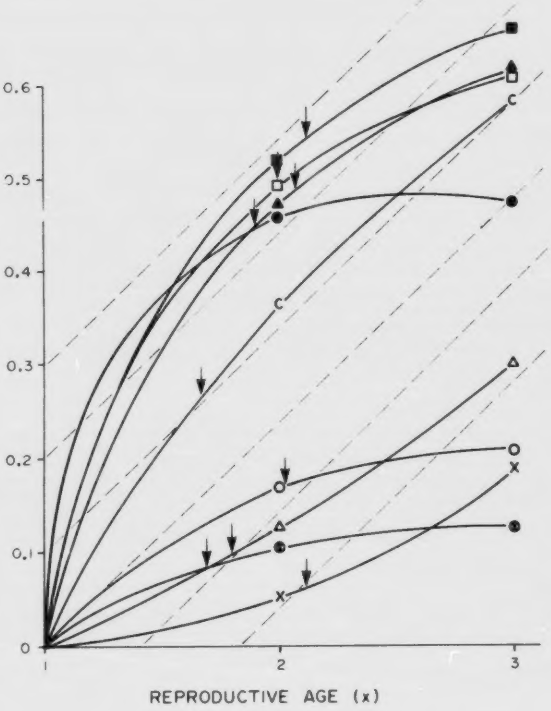

FIG. 4. Relationship between fecundity at age and natural mortality for various sockeye populations. Reproductive age is counted from the youngest mature age class of females. Change in fecundity with age is the difference between the logarithms of fecundity at reproductive age 1 and each other age. Dashed lines have slope 0.18, equal to the expected natural ocean mortality of sockeye (Ricker 1976). Fecundity curves are: (●) Cultus Lake yearling smolts and (○) Cultus Lake 2-yr-old smolts (Foerster and Pritchard 1941; Foerster 1929; (▲) Fraser River (Killick and Clemens 1963; Williams 1977); (△) Ozernaia River (Hanamura 1966); (■) Karluk Lake 2-yr-old smolts and (□) Karluk Lake 3-yr-old smolts (Hartman and Conkle 1969); (⊗)Skeena River (Dep. Fish. Oceans, unpublished data, and Bilton 1970); (c) Columbia River (Major and Craddock 1962); (X) Babine River (Aro and Broadhead 1950). See text for details of interpretation.

Several points may be made from Fig. 4. First, the relationship between fecundity and age differs considerably among populations, from those in which fecundity increases rapidly with age to those in which there is only a modest increase. Most of the curves are concave downward, as expected. Two, however, give a suggestion of being concave upward, a shape totally contrary to expectation. Given the likely errors in the data sets, however, these curves probably represent, at worst, a constant rate of increase in fecundity with age. Most important, however, from the point of view of optimum age of maturation, all but one of the populations matured at an age older than that predicted by Bell's (1980) model. According to the model, the four populations showing a slow rate of increase in fecundity with age should all have matured at the youngest possible age. Of the five populations showing a rapid rate of increase in fecundity with age, three (Karluk River adults from 2- and 3-year-old smolts and Fraser River adults) matured at an age similar to, but older than the model prediction. Cultus Lake adults from yearling smolts matured too old, however, and Columbia River blueback salmon matured too young in comparison with the model prediction.

Bell's (1980) model may also be used to examine variation in age of maturation between populations. Between populations the model predicts that fecundity per unit size should be higher in populations that mature at an older average age, to compensate for the increased mortality these populations suffer by delaying maturation. Furthermore, the rate of increase in fecundity per unit size with increasing mean age of mature females should be equal to the instantaneous rate of natural mortality.

For nine sockeye populations, whose mean age of maturation ranged from 3.6 to 6.4 years, there was no significant increase in fecundity with age. If the data point for Cultus Lake (which appears to be an outlier) is ignored, there is a significant increase in fecundity with age, but the rate of increase is still significantly less than the most probable rate of natural ocean mortality for sockeye (Fig. 5).

The optimization model is driven by the age specific patterns of mortality and natality, and its failure to make good predictions of mean age of maturation probably reflects the inadequacy of fecundity as a measure of reproductive power and contribution to future generations for sockeye. The fact that sockeye generally mature older than predicted by the model, coupled with their slow increase in fecundity with size and age, suggests that what the model fails to capture is the reproductive value of size in Pacific salmon. Healey and Heard (1984) came to the same conclusion with respect to a similar failure of the optimization model to predict age of maturation in chinook. These results suggest that in the tradeoff of energy allocation to increasing body size or egg production, increase in body size is favoured in sockeye.

The reproductive advantages of large body size have been demonstrated for female coho salmon (*O. kisutch*) by van den Berghe (1984), and similar advantages probably apply to sockeye. These include greater energy reserves for migration and nest defence, dominance on the spawning grounds so that the large females obtain the best redd sites and presumably the best mates, deeper egg burying so that the

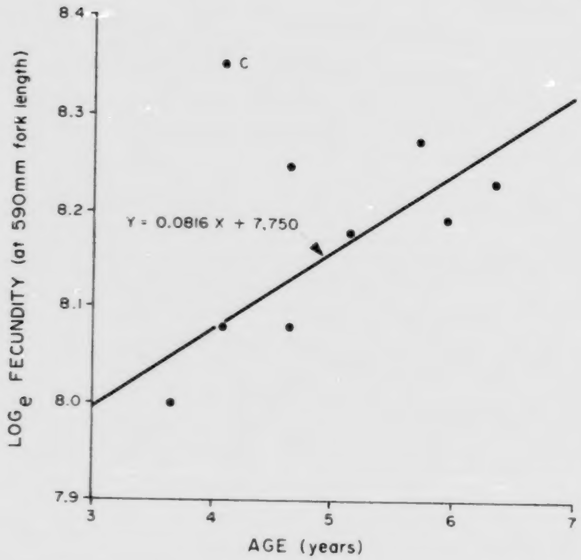

FIG. 5. Relationship between log fecundity at 590 mm fork length and mean age of females in spawning populations of sockeye. The point marked C is for Cultus Lake and the regression equation was calculated without this point. Data sources as in Fig. 4. See text for details of interpretation.

clutches are better protected from scour, superimposition and freezing, and production of larger eggs, which in turn are likely to produce larger more vigorous fry. Given these conspicuous advantages to large size in an anadromous, territorial animal like sockeye, it is not surprising that observed size and age at maturity is greater in sockeye than that predicted by a model that puts no premium on body size.

Not all sockeye populations mature at large average size, however, so that there must be circumstances that favour small size and young age at maturing. These include spawning gravel porosity (small eggs produced by small females survive better in poorer quality gravels), chronic low flows (which may affect both upstream migration and sub-gravel percolation) and high adult mortality (which favours a shorter generation time) (Healey and Heard 1985; Holtby and Healey 1986). Life history models driven by age specific patterns of natality and mortality would capture some, but not all the conditions favouring small body size.

A further shortcoming of optimization models of life history as explanations for reproductive strategies in sockeye, is more difficult to rationalize. This is their failure to account for the range of ages and sizes present in most sockeye populations. The optimization models predict a single best age (or if formulated in terms of size, single best size) of maturation. Variation around this optimum could presumably be a consequence of variable nutritional history among members of the population, both within and between years. I have, however, already indicated that this is an unsatisfactory explanation for the large within population variation in age and size at maturity in some sockeye populations. Alternate models again involved an underlying genetic cause. In the most general sense, uncertainty in the fitness value of any tactic is likely to favour strategies involving a mixture of behaviours (Real 1980).

A number of models might be proposed to account for within population variation, including conditional response to environmental variation (Stearns and Crandall 1984), and trade-offs between best male vs. best female strategies. I shall consider only two particular models that provide a potential explanation for the wide variation in age and size at maturity within sockeye populations. These are a bet hedging model and a game theory model. The bet hedging model (which falls within the optimization model category identified earlier) presumes that there is a significant risk of reproductive failure in any one year so that there is a net advantage to an iteroparous female that opts to spread reproduction over more than one year (Stearns 1976). In particular, random variation in reproductive success favours lower annual reproductive effort, lower fecundity and longer life span among iteroparous animals. In a semelparous animal, like sockeye, random variation and reproductive success could result in delayed maturity for some animals. Delayed maturity by part of a cohort would mimic the extension of reproductive life observed in bet hedging, iteroparous, animals.

The game theory model, on the other hand, presumes that, in the presence of competition for spawning sites and variable spawning gravel quality and incubation conditions, a specific mixture of female reproductive tactics will be evolutionarily stable (Holtby and Healey 1986). Essential conditions of the model are that large females must dominate small females in any contest for a redd site, and that small females must be prepared to spawn in gravel of lower porosity in areas traditionally considered to be of poorer quality than large females. Given these conditions we can imagine the following pay-off matrix for a very simplified situation involving interactions between large and small females:

	Large	Small
Large	(P1)/2	P1
Small	P3	(P2)/2

P1, P2, and P3 represent the payoff (in fitness units) to an animal of the size indicated on the left of obtaining a spawning territory when attempting to invade a population of animals of the size indicated on top. In the situation in which the established population is of large animals it is presumed that a large invader has a 50% chance of obtaining a territory whose value is P1. Thus, the pay-off for this animal is (P1)/2. When the established population is of small animals, a larger invader is certain to obtain a territory in gravel of good quality (i.e., having a high porosity and a low percentage of fine particles), so that the large invader's payoff in these circumstances is P1. When a small fish attempts to invade a population of large individuals its only option is to take a territory in gravel of a quality unacceptable to the large females, and obtain payoff P3. By an argument analagous to that for a large individual attempting to invade a population of large individuals, a small fish attempting to invade a population of small individuals will obtain a payoff (P2)/2. It also seems reasonable to presume that the following inequalities hold: P1 > P2 > P3.

For a mixture of large and small females to be an evolutionarily stable strategy it must be true that P1 > (P2)/2 and that P3 > (P1)/2. The first inequality must be true given that P1 > P2. The truth of the second inequality cannot be demonstrated from the available evidence. It is known, however, that the small eggs produced by small female coho will survive better in poor quality gravel than the large eggs produced by large female coho (van den Berghe 1984). It seems reasonable to suppose, therefore, that there is at least some gravel in most streams of a quality suitable for small females but unsuitable for large females and that most streams also have gravel suitable for large females. Thus, the conditions under which small females could invade a population of large females do occur and large females could always invade a population of small females. Once established the abundance of the invading form, whether large or small, would increase due to frequency dependent selection until the fitnesses of large and small females in the population were equal.

Gross (1984, 1985) used a game theory model to explain the existence of jack males in salmon where the competition was for females rather than nest sites. Holtby and Healey (1986) investigated the relative fitness of large and small coho in Carnation Creek, British Columbia, and concluded that a game theory model analagous to the one presented here was a sufficient explanation for size variation in female coho. They speculated that the relative frequency of large and small females in a population would be driven by spatial variation in gravel quality and by temporal variation in discharge resulting in different degrees of scour, siltation, and subgravel water exchange. A similar model seems appropriate for sockeye.

Conclusions

Sockeye females display more variation in age and size at maturity, both within and between populations, than any other *Oncorhynchus* species. The traditional environmental explanation for this variation is, in my view, unsatisfactory, although environment is certain to play a role in determining age and size at maturity.

Age (and presumably size) at maturity in sockeye is generally greater than that predicted by optimization models of life history that are driven by age specific patterns of natality and mortality. This appears to be because these models take no account of the reproductive value of large size in sockeye females. Thus, in the allocation of surplus energy among competing processes of growth and egg production sockeye seem to have allocated a greater proportion to growth and a lesser proportion to egg production. One consequence of this is that fecundity increases more slowly with increasing size in sockeye than it does in other fishes (e.g. Bagenal 1967).

Even though large size appears to be an important component of reproductive power among sockeye females, populations nevertheless display a wide range of sizes and ages at maturity. This suggests that some combination of sizes and ages confers greater fitness than a single size and age. Given the fact that various combinations of reproductive parameters appear to cluster together (i.e. large size and age, large egg size, and slightly higher fecundity; small size and age, small egg size, and slightly lower fecundity) it seems possible that the variation in reproductive tactics within a population may be explained by a game theory model. In this model small females, because of their small egg size, are able to exploit poorer quality gravels, even though they cannot compete with large females for good quality gravel. Large females, on the other hand, even though they obtain the best quality gravels for spawning, may, because they produce large eggs that have a high oxygen demand and spawn in faster flowing water, be at a disadvantage during years of unusually high or low flows because of scour or siltation in their redds. Thus, the tactics with respect to egg number and size that confer greatest fitness appear to be for small females to produce more, but smaller eggs per unit of body weight than large females. When a mixture of sizes (and ages) of fish is the best strategy and the abundance of the various size (age) categories is in equilibrium, the fitness of each will be equal. Equal fitness among female size groups appears to be confirmed for coho females in Carnation Creek (Holtby and Healey 1986), but remains to be examined for sockeye.

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Section I
Biology of Sockeye Salmon
b) Habitat and Development

Mechanisms Stabilizing Salmonid Fry Emergence Timing

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Abstract

BRANNON, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing, p. 120–124. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Water temperature during incubation of eggs exerts a major influence on the development and subsequent behavior of salmonids. The time of spawning and fry emergence within a population is related to the incubation temperature regime of their native stream. Mechanisms have evolved to synchronize the timing of these life history events with their physical environment, and are believed to have been a major factor in the development of specific stocks.

Résumé

BRANNON, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing, p. 120–124. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La température de l'eau au cours de l'incubation des oeufs influe beaucoup sur le développement et le comportement ultérieur des salmonidés. Le moment du frai et l'émergence des alevins au sein d'une population sont liés au régime thermique pendant l'incubation dans le ruisseau natal. Des mécanismes ont été développés pour synchroniser ces événements du cycle vital avec l'environnement physique; on croit que ces mécanismes sont un facteur important dans le développement de stocks particuliers.

Introduction

Members of the family Salmonidae display repetitive annual patterns of movement in space and time through an integration of genetic and environmental influences on development and behavior. The environmental component is dynamic, and this requires that response patterns based on environmental cues must incorporate a stabilizing mechanism to dampen the variation in such phenomena. Perhaps the major environmental influence on salmonid life history is temperature. As poikilotherms, salmonids are strongly influenced by the thermal regime of their habitat, and the extent of that influence is well demonstrated in the life cycle of the different species. Salmonids have adapted by synchronizing events in their life history with the temperature regimes of the rivers and lakes they use. This paper examines the influence of temperature on temporal response patterns of sockeye associated with spawning, incubation, and fry emergence. Reference is made to selected other species for comparison, and discussion is directed at mechanisms that assure synchrony between response patterns and environmental phenomena.

Methods and Materials

Major emphasis in the paper is given to Fraser River sockeye. Other species referred to are pink salmon from the Fraser River, and coho salmon and steelhead trout returning to the University of Washington hatchery, Seattle, Washington. Information on sockeye spawning and fry emergence timing, and pink salmon development rates are from the International Pacific Salmon Fisheries Commission (IPSFC, New Westminster, B.C.) records and annual reports. Mean incubation temperatures reported for streams used by the different sockeye stocks were based on thermograph records taken in the period from peak spawning to peak fry emergence. Sockeye egg measurements and incubation times were collected by the author while employed by IPSFC. Data on coho and steelhead were obtained from studies conducted at the School of Fisheries, University of Washington.

To obtain the information on sockeye egg size and incubation time to yolk absorption 20 females were sacrificed from each spawning stock selected for the study and the eggs were spawned, fertilized, water hardened, and flown to the Cultus Lake laboratory on the Lower Fraser River for incubation. Twenty eggs from each female were measured, dried, and weighed on a Mettler Gram-atic balance to determine egg diameter and weight. Data were combined to provide mean egg size information for each population.

At the laboratory, eggs taken from a particular stock were combined, subdivided in 10 small baskets of 500 eggs each, and placed in 10 troughs. The flow to each trough was set at 4 L per minute with water mixed from warm and refrigerated supplies to provide one of 10 constant temperatures, and checked twice daily. The actual temperatures experienced (1.1, 2.2, 3.3, 5.6, 7.8, 10.0, 12.2, 13.3, 14.2, and 15.6°C) varied slightly from the experimental plan because the valves controlling the water mixture could not be set precisely. Samples were taken from each basket several times over the incubation period, and the point of yolk absorption was determined to have occurred when yolk reserves were absent in 50% of the alevins remaining. Eggs incubated at 15.6°C experienced mortality throughout incubation and total mortality occurred shortly after hatching. Mortality was high in some groups held at 14.2°C also, leaving insufficient numbers to determine incubation rates. In addition eggs from two of the stocks were exposed to recirculating refrigerated water in a cooler to maintain the temperature near 0°C. Mortality was high in those groups, and the time required to reach yolk absorption at that temperature was estimated from absorption rates measured during only a portion of the incubation period.

Development rates of embryos from the early, middle, and late segments of the Cultus Lake and Weaver Creek sockeye runs, and early and middle segments of the Stellako run were obtained by spawning 5–20 females from each segment and exposing the eggs to constant incubation temperatures as described above. Egg weights were used as a measure of relative egg sizes among segments within each run.

Pink salmon embryo incubation data were obtained from the Sweltzer Creek population. Eggs were spawned from several females, fertilized with several males, combined, subdivided, and incubated nearby at the Cultus Lake laboratory in the same incubation system used for sockeye, at seven constant temperatures (1.1, 2.2, 3.4, 4.4, 5.6, 8.9, and 11.1°C). Embryos were sampled and yolk absorption determined in the same manner reported for sockeye. Embryo mortality was 100% prior to blastopore closure in groups held at temperatures below 4.4°C.

Coho salmon embryo incubation studies at the University of Washington (Dong 1981) used eggs from six Dungeness River females fertilized with sperm from four males, and divided in 10 groups each incubated at one of 10 constant temperatures (1.3, 2.4, 3.1, 4.7, 6.5, 8.3, 10.9, 12.5, 14.4, and 17.0°C). Mortality was 100% in eggs held above 12.5°C. Time for total yolk absorption was estimated by applying the rate of weight loss of visible yolk to the weight of internal yolk remaining in the final samples. Twenty eggs were used from each sample to determine yolk weight.

Steelhead embryo development rates were determined from a single University of Washington steelhead female with eggs spawned, fertilized and incubated at four temperatures (5.0, 7.4, 10.4, and 13.0°C). The incubation system and the method used to determine yolk absorption in the steelhead were the same as that used for coho.

Results and Discussion

TEMPORAL PATTERNS IN SPAWNING

Spawning time among the sockeye returning to the Fraser River covers a period of over 5 months, but each stock shows a very consistant, site-specific temporal regularity in spawning, with an annual variation around the mean of generally less than ten days (IPSFC annual reports). The temporal regularity in spawning times is related directly to the temperature regime of the streams. Late spawning stocks are found in streams with mean incubation temperatures generally in excess of 5°C. In cooler streams spawning times occur progressively earlier as the mean temperature of the incubation period decreases (Fig. 1).

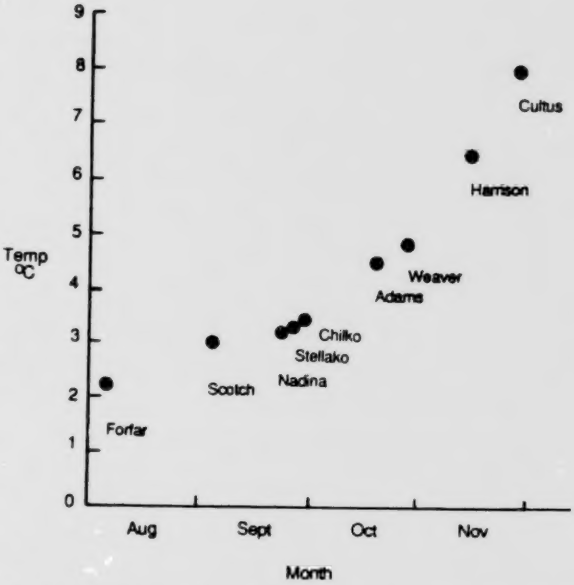

FIG. 1. Spawning times and mean incubation temperatures of nine Fraser River sockeye stocks.

Emergence timing of the fry from the redd has been identified as the major evolutionary influence that has established sockeye spawning time in a stream (Brannon 1984; Miller and Brannon 1982). As Bams (1969) postulated, the selective forces governing the time of lake entry are growth potential and food availability (to which must be added susceptibility of fry to predation), and these tend to work in opposite directions (i.e. growth potential encourages earlier entry; food availability encourages later entry) to establish emergence timing as an optimum resulting from the selective pressures affecting survival. Since the best emergence time occurs within a relatively short time interval in a given stream system, and the length of the incubation period is determined by the respective temperature regime, the appropriate time for spawning to take place becomes relatively fixed for each population. Spawning time, therefore, is a genetic characteristic of the stock which has been selected to assure optimum emergence timing under the full range of environmental conditions that pertain to each habitat.

COMPENSATION IN DEVELOPMENT RATE

Most salmonids experience a wide range in temperature during their incubation period, and because variations in the environmental cycle cannot be anticipated and adjusted for by the spawner, responses to temperature changes must be left to the developing embryo. A number of studies (Kamler and Kato 1983; Dong 1981; Alderdice and Velsen 1978; Garside 1966; Seymour 1956; Hayes and Pelluet 1945) have found that rate of development in salmonids is not constant with respect to temperature. Researchers sought formulas to describe the relationships between temperature and development rates, but did not interpret the patterns in light of the incubation needs of the species involved. *Salmo gaird-*

neri spawns in the spring on an increasing temperature regime. *Oncorhynchus* species are fall spawners and incubation usually takes place initially on a decreasing temperature regime. To accommodate the range in temperature experienced over the incubation period, and alleviate the impact of abnormal temperature variations, salmonid embryos compensate or change their development rate per unit of temperature as temperatures change.

If development was directly proportional to temperature, the rate of development per unit of temperature and the number of degree days (one degree day = 1°C> freezing/24 h) required to reach yolk absorption would be the same for all temperatures. Temperature regimes that cause abnormal variation in degree day accumulation rate would result in a severely altered emergence time. For example, spawning a week earlier than normal at a mean temperature of 14°C in the fall would accumulate 98 degree days which would accelerate emergence four weeks earlier in the spring when mean temperatures were around 3°C.

Sockeye spawn in the autumn and the incubating embryos experience the range from warm autumn to cold winter temperatures. With declining temperatures, sockeye embryo development rate increases per unit of temperature (Table 1), which helps to compensate for the fewer temperature units being accumulated. When degree days are plotted against temperature (Fig. 2), the resulting curvilinear relationship shows the increasing extent of compensation which occurs as temperatures drop below 6°C. From 15°C to 4°C, the rate of advancement per unit of temperature increases over 60%. When water temperatures drop from 4°C to freezing, compensation increases nearly 800%, permitting development to proceed with relatively little loss of time. In this manner sockeye are much less influenced by variability in the incubation temperature pattern, and the severe effects of prolonged low temperatures are substantially tempered.

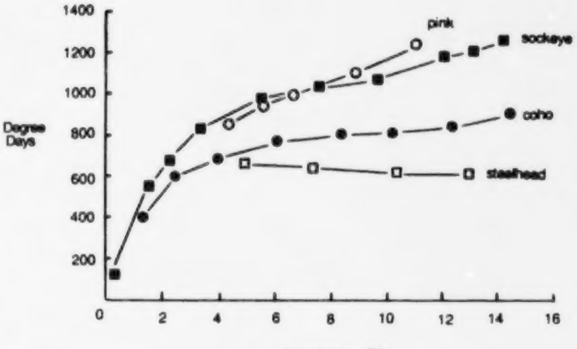

FIG. 2. Relationship between temperature (°C) and degree days to yolk absorption for salmon and steelhead incubated at constant temperatures.

Compensation as a control mechanism is also demonstrated in other salmonid species. Pink salmon spawn in the late summer–early fall part of the temperature cycle. This is generally earlier than sockeye when in the same stream, but both species experience similar incubation conditions and emergence timing. Degree day requirements to emergence are higher for pinks at warm temperatures, and they approximate those for sockeye at lower temperatures (Fig. 2). This appears to indicate that pinks have altered their development rates over the range of incubation temperatures in order to relate to somewhat different incubation habitat.

In contrast to sockeye and pinks, coho salmon are generally very late fall spawners, and they confront a low range of

TABLE 1. Development rates to yolk absorption of nine Fraser River sockeye stocks incubated at 10 constant temperatures.

Stock		Temperature °C										Egg dry wt. mg	
		0.25	1.6	2.3	3.4	5.6	7.6	9.7	12.1	13.1	14.2	$\bar{X}$	(SD)
Chilko	D[a]		347	293	243	179	135	111	98	96		40.43	(3.86)
	U		555	674	826	1 002	1 026	1 078	1 186	1 258			
Cultus	D		312	273	225	163	128	106	92	84		33.07	(2.85)
	U		499	628	765	913	973	1 028	1 113	1 100			
Harrison	D		360	330	268	192	143	122	108			65.08	(7.40)
	U		576	759	911	1 075	1 087	1 183	1 307				
Horsefly	D		345	281	240	172	132	104	93	89	86	35.06	(2.27)
	U		552	646	816	963	1 003	1 009	1 125	1 166	1 221		
Nadina	D	442[b]	311	262	218	160	126	99	87	85	83	33.55	(3.29)
	U	111	498	603	741	896	958	960	1 053	1 114	1 179		
Pitt	D		378	335	274	197	153	127	113	105	101	61.37	(6.48)
	U		605	771	932	1 103	1 163	1 232	1 367	1 376	1 434		
Raft	D	447[b]	338	293	247	174	137	110	96	95		41.67	(3.55)
	U	112	541	674	840	974	1 041	1 067	1 162	1 244			
Stellako	D		316	260	218	157	125	101	92	88	85	33.59	(2.94)
	U		506	598	741	879	950	980	1 113	1 153	1 207		
Weaver	D		326	284	240	172	133	108	95	90	85	46.73	(3.90)
	U		522	653	816	963	1 011	1 048	1 150	1 179	1 207		

[a] D = days, U = degree days.

[b] Calculated from incomplete data.

temperatures during the entire incubation period. Consequently this species has evolved a more rapid rate of development (Fig. 2) to reach optimum emergence timing in the early spring. The relationship between degree days and temperature (Dong 1981) reflects the late fall spawning pattern of coho. Demonstrating the same degree of compensation in rate of development as sockeye at the lowest temperatures, the relationship flattens between 6°C and 13°C which is a temperature range that exceeds the stream temperatures coho normally experience during incubation and where compensation would have had less need to evolve.

Even further contrast is seen in the incubation temperature requirements of steelhead trout. Steelhead are late winter–early spring spawners, and they have evolved a rate of development that is even faster than coho, although they emerge later. Compensation in steelhead rate of development is particularly interesting because the relationship between degree days and temperature tends to have a reversed slope to that for salmon (Fig. 2). As temperatures increase, the rate of development per unit of temperature also increases. This results in slightly fewer temperature units required to reach a comparable stage of development when at higher temperatures than at lower temperatures. Although data were obtained from only one steelhead egg lot, development rates compared favorably with those reported for rainbow trout (Leitritz and Lewis 1976). The pattern relates to the spring spawning behavior of the species which places incubation on the increasing phase of the temperature cycle, and where warming temperatures would indicate more favorable emergence conditions.

Compensation is a mechanism that tends to stabilize the development rate of salmonid embryos when exposed to a wide range in temperature during incubation. Compensation also reduces the distortion that abnormal spawning time or variability in temperature regimes would have on emergence timing. The pattern in compensation is species-specific, which means that metabolic rates at different temperatures have evolved under the ecological constraints peculiar to each species.

Influence of Egg Size on Incubation Time

There is considerable variation in egg size within each salmonid species. In Fraser River sockeye, for example, mean egg weight in stocks with large eggs is nearly twice that of stocks with small eggs. Large eggs produce larger fry and generally more time is required to complete yolk absorption than with smaller eggs (Table 1). When such large variation in egg weight exists, differences in size could be a mechanism to influence the length of the incubation period and thus further affect emergence timing.

The time required for yolk absorption in fry resulting from eggs of different populations is correlated with egg size ($r = 0.88$), but it isn't always proportional to egg size. For example in the experimental data on Table 1, Weaver eggs weighed 41.3% more than Cultus eggs and were heavier than those from Chilko, but they incubated only up to 7% longer than Cultus eggs and required less time than Chilko eggs. Similarly, Harrison sockeye eggs were heavier than Pitt eggs, but required less time to reach yolk absorption. Clear support for egg size as a mechanism to influence incubation time isn't apparent from the data comparing populations.

Further uncertainty regarding the influence of egg size on incubation time concerns the amount of variation in egg weight that exists within a stock. If the variation in incubation time was directly proportional to variation in egg weight, the length of the incubation period for a stock would have been determined by selection of the appropriate egg size, and variability would be minimal. However, there appears to be little supporting evidence for the hypothesis. Egg weight variation among 4-yr-old spawners in a given year can range in excess of 30%, and the mean egg weight of a spawning stock can vary from year to year by as much as 15%. Moreover, comparing different egg lots within a stock has shown that time to yolk absorption is very similar and not correlated with egg weight (for example, $r = 0.29$ in 15 Weaver Cr. egg lots). Therefore, while incubation times among sockeye stocks appear to be related to egg size, it is believed that differences in egg size relate primarily to reproductive strategies other than timing.

Timing Patterns Under Constant Incubation Temperature

In some instances sockeye populations spawn on upwelling areas where incubating eggs are irrigated with ground water at nearly constant temperature. Under these circumstances development rate is fixed, and the variation in emergence timing will occur primarily from the variation in the time of egg deposition. Consequently, embryos have no opportunity to compensate their rate of development to coordinate emergence with the ambient conditions of their rearing area. Timing will approach optimum for a segment of the emergence curve only as frequently as it fortuitously corresponds with the seasonal weather conditions that determine nursery lake readiness. With highly variable spring weather conditions that occur from year to year in the Pacific Northwest, different segments of the emergence curve would be favored sufficiently often to sustain their associated spawning times, and the sockeye population would assume a long spawning period. Cultus Lake sockeye are believed to have assumed such a strategy.

The population spawns on Lindell Beach, a spring-fed alluvial fan at the south end of the Cultus Lake basin. Water temperatures irrigating the beach are nearly constant at 8°C throughout incubation. Adults begin spawning on the beach before the first of November and continue to January, extending beyond the normal spawning range of other sockeye populations by at least 4 wk. Since the irrigating water isn't affected by weather conditions, embryos have no opportunity to compensate their rate of development for variation in surface water temperature. Therefore, a long spawning period is sustained because each year a different segment of the emergence curve is favored.

Further evidence of the complexity of timing strategies is evident in the development rates of eggs from different segments of the Cultus population. In three different brood years, eggs of similar weight were taken from early, middle, and late segments of the spawning populations and incubated at 8°C. In each instance, the early segments required several days more incubation time than the late segments, with the center segments intermediate to the extremes (Table 2). The trend in development rates had the effect of reducing the spread that would otherwise occur in spawning

TABLE 2. Development rates to yolk absorption of Cultus Lake sockeye from early, medium, and late run segments incubated at 8°C.

Date spawned	Days incubated to yolk absorption	Degree days acquired
1963		
11/15	130	1 040
11/29	124	992
12/14	123	984
12/27	119	952
1964		
11/06	132	1 052
11/20	127	1 016
12/08	123	984
1966		
11/02	137	1 096
11/25	127	1 016
12/14	120	960

time. For example in 1966 the 43-day period representing the range in egg collection dates was reduced by 17 days at emergence. Examination of other sockeye populations showed no difference between development rates of early and late spawners, which suggests that the response in the Cultus population is a unique adaptation to that particular situation.

The timing pattern of lake spawning sockeye in Cultus Lake, therefore, appears to have been influenced by two circumstances. First, with no opportunity to compensate for seasonal weather conditions that determine nursery lake readiness, the spawning population spreads over a broad time range facilitated by the irregular selective advantage each segment has received when it met with favorable emergence timing on different years. Second, the range in the spawning time was an advantage in the presence of limited spawning area. The primary spawning area in Cultus Lake is small, occupying less than 2 000 square metres for recorded populations of 37 000 fish (IPSFC 1950) and with historic levels probably much larger. Under very high densities the population expanded its spawning time by occupying the limited area sequentially, with the early and late extremes of the population developing at respectively slower and faster rates to align their emergence time with the more optimum central emergence timing. Such patterns suggest that Cultus sockeye consist of temporally isolated sub-stocks that may have survived because Cultus Lake is a very productive basin (Goodlad et al. 1974).

The existence of mechanisms controlling temporal patterns in salmonid behavior to achieve synchronized emergence with the environmental events of their habitat indicates the importance of emergence timing to these species. Emergence timing is considered here to be the major selective force influencing time of spawning and the biochemical relationships which compensate embryo development rate for variation in incubation temperature. Genetic mechanisms have evolved to stabilize emergence timing under the environmental conditions specific to a stock to help assure maximum fry survival. These mechanisms also influence other life history characteristics, such as migratory behavior and perhaps distribution. The critical relationships that salmonids demonstrate with their environment emphasizes the need for management to include measures to preserve the uniqueness that stocks have acquired.

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Influence of Environment on the Abundance of Sockeye Salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka Rivers

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Abstract

Selifonov, M. M. 1987. Influence of environment on the abundance of sockeye salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka rivers, p. 125–128. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Variations in egg mortality and abundance of progeny of sockeye salmon (*Oncorhynchus nerka*) were studied in relation to changes in hydrometeorological conditions in the Kurile Lake area. Water level and temperature regimes during the period of egg development influence the abundance of Ozernaya sockeye. Fluctuations in abundance of these sockeye are also correlated with long-term changes in solar activity.

Résumé

Selifonov, M. M. 1987. Influence of environment on the abundance of sockeye salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka rivers, p. 125–128. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

On étudie les variations de la mortalité des oeufs et de l'abondance des alevins de saumon nerka (*Oncorhynchus nerka*) par rapport aux fluctuations des conditions hydrométéorologiques de la région du lac Kurile. Le niveau d'eau et les régimes thermiques pendant la période de développement des oeufs influent sur l'abondance du saumon nerka de l'Ozernaya. Les fluctuations de l'abondance de l'espèce sont aussi liées aux variations à long terme de l'activité solaire.

The abundance of Pacific salmon fluctuates considerably according to both fishing intensity and hydrological and meteorological conditions during the period of egg development and fish growth in fresh water. Environmental factors have been studied in relation to many populations of salmon, particularly in relation to the efficiency of reproduction of chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon. Temperature and flow regimes and the depth of snow cover have been recorded for different areas of the continental coast of the Okhotsk Sea, the Amur River basin, and Sakhalin (Kostarev 1964; Levanidov 1964, 1968; Gritsenko 1967; Rosly 1972).

Different non-biological factors are thought to influence spawning efficiency in different spawning areas. Survival of chum and pink salmon eggs is known to be closely related to September–October discharge in some streams (Foerster 1955; Hunter 1956). Kostarev (1964) found correlations between the number of chum salmon progeny on the continental coast of the Okhotsk Sea and both the depth of snow cover and air temperatures in corresponding brood years. Nikolaeva (1983) found positive correlations between returns of Kamchatka River chum salmon and January precipitation, February snow depth, and March water level. The survival rate of Kamchatka River chinook salmon eggs is positively correlated with flow regime but the ratio of returns/spawner is negatively correlated with water temperature and precipitation in the autumn–winter period (B.B. Vronskyi, pers. comm.). Grachev (1978) found that air temperature and precipitation exert variable influences on pink salmon reproduction in different areas of the Kamchatka peninsula; in some areas the influence of these factors is strong, in others it is weak. Krogius (1951) found that environmental factors such as freezing and silting could result in almost complete mortality of Lake Dalnee sockeye eggs, and Bugaev (1983) showed that in most instances there was a high correlation between returns/spawner and air temperature at the start of egg incubation in summer.

In many cases it is difficult to find any connection between environmental conditions and population abundance. Long-term climatic variations, particularly solar activity which is correlated with various hydrological and hydrometeorological conditions, have also been examined. The existence of a relationship between solar activity and salmon abundance was first suggested by Birman (1966, 1969, 1973) and later demonstrated by Davydov and Zorbidi (1978) for eastern Kamchatka coho salmon (*O. kisutch*).

Papers have already been written on the influence of hydrometeorological conditions on the production of sockeye from the Kamchatka river (Krogius 1949, 1951; Simonova 1972; Bugaev 1983). The sockeye salmon run to Kurile Lake in the Ozernaya River basin has been less studied in this respect, though it is one of the largest stocks of sockeye salmon on the Asian coast. The Ozernaya sockeye salmon population fluctuates considerably from 260 to 4 200 thousand spawning adults and 1 200 to 9 350 thousand total returns. The numerical relationship between spawners (S) and progeny (R) is non-linear, expressed by the equation; $R = aSe^{-bS}$ (Ricker 1971). However, there is considerable variation in numbers of progeny produced by a given number of spawners. Thus 500 thousand spawners in each of 1955 and 1958, produced a threefold difference in numbers of progeny. Environmental conditions are probably implicated in such cases. The purpose of this paper is to show how the environment influences the abundance of Ozernaya sockeye salmon.

Methods

Hydrometeorological data were collected at the Ozernaya observation site in the vicinity of Kurile Lake during 1946–1979. These data were examined for correlations with records of sockeye egg mortality during development in the gravel, and with the size of spawning escapements and total returns. Hydrometeorological data included: (1) air temperatures: (a) average annual, (b) minimum, (c) maximum, (d) average monthly in May, (e) average monthly in November, (f) average monthly in December; (2) water temperatures: (a) average annual, (b) minimum, (c) maximum, (d) average in May; and (3) water levels: (a) average annual, (b) minimum, (c) maximum, (d) difference between September and May monthly averages, (e) difference in August and May monthly averages, (f) September average, and (g) February average.

To reveal the cyclic nature of fluctuations, time series data were smoothed using a weighted running average (Plokhinsky 1961). Woolf's number (Pavlychev 1977) and data on signs of the sun's magnetic field (Miroshnichenko 1976) were used to describe solar activity.

Results

When redds were examined in spring on spawning grounds at Kurile Lake, it was apparent that egg mortality had occurred early in the developmental period. Mortality was low among advanced alevins but many dead alevins were found in some years. Thus, I consider the critical periods in early ontogenesis of sockeye salmon to be at the time of deposition and later during very early development of hatched alevins. I therefore recorded water temperatures and levels at these critical times.

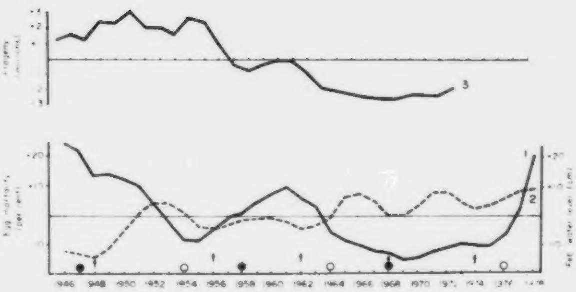

FIG. 1. Smoothed curves of annual egg mortality (1), water level in February (2), and year-class abundance (3) expressed as deviations from the long-term mean. Open circles indicate minimum solar activity, closed circles indicate maximum solar activity and arrows indicate minimum water levels.

In most cases air and water temperatures (indices 1 a–d and 2 a–d) were themselves correlated (Table 1). Water level indices (3 a–g) are also interrelated. However, there is very little correlation between water level and temperature indices.

The following hydrometeorological features of the Kurile Lake area are worth noting: (1) air temperature indices have essentially a 4-yr cycle; (2) water temperature indices usually have a 6-yr cycle; and (3) water levels commonly have a 5-yr cycle. Such non-synchronized cyclic patterns serve to obscure their respective influences on the abundance of Ozernaya sockeye salmon. Only the negative correlations between returns/spawner and average annual water level ($r = -0.34$), minimum water level ($r = -0.31$), and water levels in September ($r = -0.32$) were significant.

However, after smoothing the data for egg mortality, February water levels, and numbers of progeny in corresponding brood years, some perceptible relationships emerge (Fig. 1). Egg mortality has three distinct peaks — 1945, 1961, and 1978 — and the minimum water levels in February are repeated with almost precise six year periodicity. Egg mortality increases when water levels fall below the long-term mean and abundance of progeny (R) is either relatively high or average (see 1943–52; 1958–63).

Egg mortality is low during periods of minimun solar activity (see 1954, 1964, 1976). If escapements had been larger

TABLE 1. Correlation coefficients between various indices of hydrometeorological conditions

Indices	1-b	1-c	1-d	2-a	2-b	2-c	2-d	3-a	3-b	3-c	3-d	3-e	3-f	3-g
1-a	0.57	0.57	0.57	0.48	0.23	0.38	0.44	0.00	0.21	−0.18	−0.07	−0.29	−0.08	−0.31
1-b		0.01	0.14	0.47	0.38	0.63	0.48	−0.04	0.41	−0.17	0.25	0.21	0.19	−0.39
1-c			0.39	0.31	0.34	−0.20	−0.11	−0.01	0.00	−0.05	−0.11	−0.38	−0.03	−0.17
1-d				0.39	0.24	0.28	0.30	0.34	−0.08	−0.08	0.08	−0.29	0.02	0.18
2-a					0.79	0.61	0.67	−0.11	0.13	−0.31	0.14	−0.01	−0.01	−0.47
2-b						0.39	0.39	−0.22	−0.09	−0.26	0.37	0.02	−0.07	−0.29
2-c							0.57	0.00	0.30	−0.26	0.19	0.27	0.18	−0.38
2-d								0.08	0.40	−0.37	0.25	0.22	0.19	−0.41
3-a									0.44	−0.78	−0.20	−0.25	0.66	0.49
3-b										0.21	0.04	0.34	0.57	−0.21
3-c											−0.40	−0.41	0.44	0.61
3-d												0.59	0.31	−0.20
3-e													0.06	−0.44
3-f														0.28

from 1968 to 1972, egg mortality would likely have increased during the last interval between periods of low solar activity. However, neither of these occurred.

Abundance of progeny was not correlated with egg mortality before 1959. The nineteenth solar cycle was one of very high activity with a maximum in 1957–58. A positive linear relationship ($r = +0.91$) between egg mortality and spawning escapement has been observed from 1959 to the present. Recent egg mortality was more closely related to spawner abundance than it was earlier in the period (Fig. 2) but the correlation was high throughout. The number of mature spawners varied considerably and periods of low abundance were associated with minimal solar activity in an inexplicable way. It is puzzling because spawner abundance is influenced by fishing intensity which has only recently been regulated; in the past, exploitation rate has varied from 33 to 94% of the maturing fish. However, the relationship between total abundance and numbers maturing in the same brood year has not been close ($r = +0.39$).

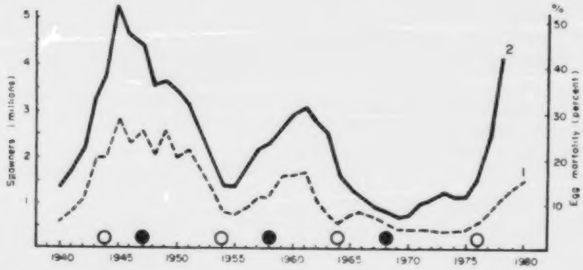

FIG. 2. Smoothed curves of spawner abundance (1) and egg mortality (2). Open circles indicate minimum solar activity, closed circles indicate maximum solar activity.

Ratios of returns/spawners smoothed by a moving average of five years showed a periodicity of 7–8 years (Fig. 3) but there was a 14-yr period between the 1941 and 1955 peaks. However, a period of high solar activity occurred in 1947 and returns/spawner are reduced in such periods. No linear relationship between returns/spawner and water temperature has been demonstrated, but when interannual variations are plotted, returns/spawner were noticeably larger during periods when solar activity was low and water level at the end of egg development was high.

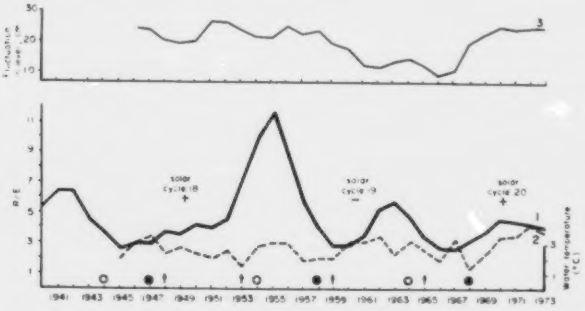

FIG. 3. Smoothed curves of the ratio of returns/spawner (1), water temperature in May (2) and difference in water levels in September of the year of spawning and in May of the following year (3). Open circles indicate minimum solar activity, closed circles indicate maximum solar activity and arrows indicate years of lowest water temperature.

There was a long-term relationship between ratios of returns/spawner and seasonal differences in water level. Water levels declined during the period from egg deposition in approximately September to emergence in May (Fig. 3), and over a period of nearly 30 years returns/spawner have been larger as the difference between September and May water levels increased. Since this difference in water levels affects discharge, it may be said that the higher the discharge, the higher egg survival, and ultimately, the larger the return of affected year-classes.

Increasing trends in returns/spawner were not the same in all solar cycles. When a cycle with a positive magnetic field changed to a negative one, returns/spawner were maximal. Conversely, when the field changed from negative to positive, returns/spawner have exceeded the mean value by a factor of only 1.5–2. Furthermore, in even cycles (18 and 20) increases in parental abundance and egg mortality occurred on the ascending limbs of peak solar activity and in odd cycles (19 and probably 21), on the descending limbs.

Conclusions

1) Cyclic patterns have occurred in time series of several hydrometeorological indices in the Kurile Lake area: air temperatures followed a 4-yr cycle, water temperatures followed a 6-yr cycle and water levels followed a 5-yr cycle.

2) Egg mortality increased when water levels fell below the long-term mean for both average and above average spawning escapements.

3) Egg mortality was positively correlated with spawning escapement but less closely at high abundance than at low abundance ($r = +0.91$). Thus, the extent of egg mortality depended on spawner abundance but this mortality was most significant in years of low abundance.

4) Ratios of returns/spawner increased with increasing differences between water levels at the time of egg deposition (September) and fry emergence (May).

5) Water levels and temperatures during periods of egg development may be used to forecast abundance of Ozernaya sockeye salmon.

6) A relationship exists between fluctuations in Ozernaya sockeye abundance and long-term solar changes. In periods of minimum solar activity, sockeye abundance, egg mortality, and coefficients of returns/spawner were reduced. Recruitment is probably determined by the interaction between numbers of spawners and conditions influencing the development and growth of eggs and juveniles.

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Factors Influencing Age and Growth of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in Lakes[1]

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Abstract

BURGNER, R.L. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes, p. 129–142. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

A review of data from sockeye-producing lakes revealed large differences in growth rate among populations of juvenile sockeye (*Oncorhynchus nerka*) and in age composition of smolts. These differences result in part from quite persistent differences in lake nutrient supply and food, and in part from varying differences in physical conditions such as water temperature, growing season, and light penetration. Age at seaward migration and some behavior patterns influencing rearing area utilization quite obviously have racial, or genetic, components apparently related to historical conditions for survival in the lake system. Within a sockeye lake, growth rate and age at seaward migration may be affected by population pressure, but annual differences may also result from between-year differences in climatic conditions. Some populations show no evidence of population effects on growth or age at seaward migration at existing population levels. Although competitor species such as threespine stickleback (*Gasterosteus aculeatus*) may exert an influence on juvenile sockeye growth and production in some sockeye lakes, juvenile sockeye greatly predominate in their feeding areas in most sockeye lakes, particularly in the limnetic zone. Therefore, where indications of competition are evident, the intraspecific component is likely to be much stronger than the interspecific component.

Résumé

BURGNER, R.L. 1987. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes, p. 129–142. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Une étude des données sur les lacs producteurs de saumon nerka (*Oncorhynchus nerka*) a révélé d'importantes variations du taux de croissance chez les populations de saumon nerka juvénile et de la composition par âge des smolts. Ces différences sont le résultat, d'une part, de variations persistantes de l'apport de bioéléments et de matières nutritives dans le milieu lacustre et, d'autre part, de divers écarts entre les conditions physiques dont la température de l'eau, la saison de croissance et la pénétration de la lumière. L'âge à la dévalaison et certains comportements influant sur l'utilisation des zones d'alevinage ont selon toute évidence certaines composantes raciales ou génétiques manifestement liées aux conditions historiques pour la survie dans le système lacustre. Dans un lac à saumon nerka, la pression démographique peut influer sur le taux de croissance et l'âge au moment de la dévalaison quoique des différences annuelles puissent aussi être le résultat de variations des conditions climatiques d'une année à l'autre. Certaines populations ne montrent aucun signe de répercussions démographiques sur la croissance ou l'âge à la dévalaison au niveau actuel des effectifs. Des espèces compétitrices comme l'épinoche à trois épines (*Gasterosteus aculeatus*) peuvent exercer une influence sur la croissance et la production de saumons nerkas juvéniles dans certains lacs, mais ces saumons sont en plus grande abondance dans l'aire d'alimentation de la plupart des lacs à saumon nerka, surtout dans la zone limnétique. Par conséquent, là où une compétition est évidente, la composante intraspécifique sera probablement plus importante que la composante interspécifique.

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[1] School of Fisheries Contribution No. 717.

Introduction

The annual growth attained by juvenile sockeye and their length of residence in fresh water vary greatly among populations in different lake systems around the North Pacific rim as well as between years within individual lakes. Freshwater growth and age at seaward migration often reflect the factors controlling production of juvenile sockeye in individual lakes and lake systems. I will present examples of differences among and within populations in growth and freshwater age, and will discuss possible causes, including density-dependent and density-independent limitations on growth within the rearing environment.

Size and Age at Seaward Migration

SMOLT SIZE

At the beginning of their lake life, sockeye fry are between 25 and 31 mm in length and weigh between 0.1 and 0.2 g (McDonald and Hume 1984; LeBrasseur et al. 1978; Rogers 1979), but their subsequent growth rate varies widely among populations. Comparative size data for sockeye smolts demonstrate the wide range among lake populations in freshwater growth (Table 1). Lakes producing large yearling smolts include Hidden and Big lakes in Cook Inlet, Frazer Lake on Kodiak Island, Lake Washington, and Lake Dalnee in east Kamchatka. Populations in Frazer Lake and in Lake Washington developed from introduced sockeye runs. In the initial few years following transplants of sockeye from Red and Karluk river systems, Frazer Lake smolts migrating at age 1. averaged about 15 cm in length and 30 g in weight, and smolts migrating at age 2. averaged nearly 18 cm long and about 54 g in weight (Blackett 1984). (Average sizes have declined over the years as the juvenile sockeye population in the lake increased.) Lakes producing small yearling smolts, averaging less than 6.7 cm long and 2.7 g in weight, include Falls Lake on Baranof Island, Kennedy on Vancouver Island, Tokun in the Copper River delta, Little Kitoi on Afognak Island, and Kenai in Cook Inlet. The smallest yearling (averaging only 6 cm and 2 g) are found in the glacial waters of Owikeno Lake, coastal British Columbia (Ruggles 1966). Mean weights of yearling smolts in Frazer Lake and Lake Washington are about 11 and 9 times as heavy, respectively, as the mean weight of yearling Owikeno smolts (Table 1). Smolts of intermediate size are produced in the large sockeye lakes of interior British Columbia, Bristol Bay and Kamchatka.

AGE OF SMOLTS

There seems to be no general rule regarding threshold size for smoltification among populations. Growth does influence duration of stay in fresh water before smoltification, and within lake populations the larger members of a year-class tend to migrate to sea earlier in the spring or (usually) to migrate a year earlier than smaller members (Barnaby 1944; Krogius and Krokhin 1948; Burgner 1962a; Foerster 1968). In the more southern lake systems such as those in the Fraser River watershed, smoltification after one year of lake residence is nearly universal, with few carry-overs for another year (Killick and Clemens 1963; Foerster 1968). In Bristol Bay there is much variability in age at smoltification both among lake system populations and among brood-year-classes within lake systems (e.g., Iliamna–Clark system, Rogers and Poe 1984). Size is not strictly the determinant for duration of stay in freshwater, since some populations with very poor freshwater growth in their first year migrate predominantly as yearlings (e.g., Lake Owikeno, Lake Tokun), while other populations exhibiting good first year growth migrate predominantly after a second year of lake residence (e.g., Lake Becharof, Bristol Bay). The Lake Washington sockeye, being of large size, do migrate as yearlings, yet strangely, the yearling sockeye of Frazer Lake, Kodiak Island, mainly remain an additional year in fresh water before smoltification in spite of their phenomenal first year growth. Their tendency to migrate at an older age may be a genetic carry-over from the source stocks (Karluk and Red lakes), which smoltify primarily at age II.

In Table 2 the most common age-groups in adult returns to different lake systems are presented for background information. They are listed in order of abundance for each system. For individual lake systems, age at seaward migration often influences length of stay in the ocean.

Lake Environment

NUTRIENTS AND FOOD SUPPLY

It is evident that food supply and other conditions for juvenile sockeye growth are much better in some sockeye pro-

TABLE 1. Comparative size data for sockeye smolts from various lake systems.

Lake or lake system	Age	Mean length (mm) No. yr.	Avg.	Range	Mean weight (g) No. yr.	Avg.	Range	Source
Washington state								
Washington	1	4	125	120–129	4	18.5	16.7–26.5	Bryant (1976)
Fraser River								
Cultus	1	21	82	68–94	21	6.2	3.0–8.6	Eggers (1978)
Chilko	1	20	82	73–101	20	4.6	3.1–8.4	Eggers (1978)
Fraser	1	1	90	—	1	7.8	—	Goodlad et al. (1974)
Shuswap	1	7	74		7	4.0		Goodlad et al. (1974)
B.C. Coastal								
Babine (main l.)	1	22	79	75–83	22	4.9	4.9–5.8	H.D. Smith, pers. comm. Canada Dept. Fisheries and Oceans, 1090 W. Pender St. Vancouver, BC. V6E 2P1

TABLE 1. Comparative size data for sockeye smolts from various lake systems. (*Continued.*)

Lake or lake system	Age	Mean length (mm) No. yr.	Avg.	Range	Mean weight (g) No. yr.	Avg.	Range	Source
Owikeno	1	4	60	59–61	1	2.0	—	Ruggles (1966)
Long	1				5	2.7	1.2–4.9	Hyatt and Stockner (1985)
Vancouver Is.								
Great Central	1	8	69	64–78	9	3.8	2.7–5.3	LeBrasseur et al. (1978)
	2				6	8.1	4.0–14.3	LeBrasseur et al. (1978)
Kennedy	1				1	2.6	—	Hyatt and Stockner (1985)
Henderson	1				5	3.2	2.3–4.3	Hyatt and Stockner (1985)
Hobiton	1				5	4.0	3.3–4.8	Hyatt and Stockner (1985)
S.E. Alaska								
Falls	1	1	67		1	2.4		Koenings et al. (1984)
	2	1	70		1	2.8		
	3	1	76		1	3.5		
Copper R.								
Summit	1	1	92					Roberson and Holder (1987)
Tokun	1	2	65	63–67	2	2.3	2.1–2.4	McDaniel et al. (1985)
Prince WM. SD.								
Eshamy	1	2	75	73–77	2	3.5	3.2–3.7	McDaniel et al. (1985)
	2	2	99	97–100	2	7.8	7.1–8.4	
Cook Inlet								
Larson	1	1	77	—	1	3.7	—	Lebida (1984)
Hidden	1		143			27.3		Koenings et al. (1984)
	2		200			83.9		
Big	1		132			25.5		Koenings et al. (1984)
	2		166			48.1		
Russian	1		84			5.1		Koenings et al. (1984)
	2		93			6.5		
Kenai	1		62			2.1		Koneings et al. (1984)
	2		72			3.1		
Crescent	1	2	69	68–69	2	2.8	2.7–2.8	Koenings et al. (1985)
	2	2	76	76–76	2	3.7	3.6–3.8	
Kasilof	1	5	70	68–73	5	2.9	2.7–3.3	Flagg et al. (1985)
	2	5	85	82–90	5	5.1	4.8–5.3	Flagg et al. (1985), fig. 7, 8
Packers	1	3	83	74–96	3	5.2	3.4–7.9	Koenings and Burkett (1987b)
	2	3	97	88–104	3	7.5	5.4–9.4	
	3	1	113		1	11.6		
Tustumena	1	5	70	68–73	5	2.9	2.8–3.3	Koenings and Burkett (1987b)
	2	5	85	82–88	5	5.1	4.8–5.2	
Kodiak-Afognak								
Karluk	1	11	111	100–122				Barnaby (1944), years
	2	12	134	127–142				1925–1936
	3	12	144	137–152				
	1	5	107	102–110	5	12.7	10.7–14.5	Drucker (1970), years
	2	8	118	113–128	8	15.0	12.4–21.0	1961–1968
	3	8	130	123–142	8	19.9	15.3–26.7	
	1	4	102	96–112	4	10.8	8.3–14.8	ADF&G (1979–1982)
	2	4	113	103–120	4	14.1	9.4–18.5	
	3	4	128	113–147	4	19.3	11.7–29.1	
Red	1		85			5.8		Koenings et al. (1984)
	2		111			12.8		
Frazer	1	14	135	113–163	14	22.7	12–35	Blackett (1984)
	2	14	162	142–185	14	39.1	23–62	
	3	9	185	154–201	5	51.4	30–76	
Little Kitoi	1	6	64	43–75				Meehan (1966)
	2	6	72	69–83				
Ruth	1	5	104	88–119				Meehan (1966)
	2	5	125	114–137				
Bristol Bay								
Wood River	1	24	83	71–91	5	5.2	3.5–7.6	Bucher (1984)
	2	22	100	90–114	5	8.6	6.8–10.1	
Iliamna-Clark	1	28	88	80–98	25	5.9	4.2–8.4	Bill (1984)
	2	27	109	97–122	25	10.9	7.5–16.4	
	3	1	124	—	1	17.5	—	

TABLE 1. Comparative size data for sockeye smolts from various lake systems. (*Continued.*)

Lake or lake system	Age	Mean length (mm) No. yr.	Avg.	Range	Mean weight (g) No. yr.	Avg.	Range	Source
Naknek	1	23	100	91–113	23	9.1	6.9–13.1	Huttunen (1984a)
	2	23	112	100–120	23	12.6	10.1–14.7	
	3	3	121	109–131	2	21.3	19.1–23.5	
Becharof	1	7	103	99–107	2	9.2	9.1–9.2	Bue (1984)
	2	7	120	115–130	2	15.8	14.6–17.1	
	3	7	129	115–145	2	21.3	19.1–23.5	
Ugashik	1	16	91	81–97	16	6.5	5.0–7.7	Eggers (1984)
	2	16	114	104–125	16	12.4	9.6–15.9	
	3	4	131	125–138	4	18.4	14.3–22.5	
Kamchatka								
Dalnee	1	7	116	106–133	7	16.4	12.5–23.0	Krogius and Krokhin (1948)
Kuril	2	12	93	85–102				Selifonov (1970)
	3	12	108	98–116				

TABLE 2. The most common age-groups of sockeye salmon, by river system. (Underline indicates age-group is always predominant. Inclusion of an age-group indicates it has exceeded 20% in one or more of years examined).

River system or stock	Age-groups	Remarks	Source
Washington			
Columbia R.	1.2, 1.1		Anas and Gauley (1956)
Quinault R.	1.2, 1.3		Johnson (1977)
L. Washington	1.2		
British Columbia			
Fraser R.	1.2	Catch samples 1915–60	Killick and Clemens (1963)
Harrison R. (Fraser)	0.2		
Skeena R. (Babine L.)	1.3, 1.2	Variable, on the average about equal. Brood 1961–77 returns	McDonald and Hume (1984)
Nass R.	2.2, 1.2		Foerster (1968)
Rivers Inlet	1.3, 1.2	5 years	Healey (1987)
Smith Inlet	1.3, 1.2	5 years	Healey (1987)
S.E. Alaska			
Chilkoot	1.3	1976–82	Bergander (1985)
Chilkat	1.3, 2.3, 2.2	1976–82	Bergander (1985)
East Alsec. R.	0.3, 0.2	1981–83	McBride and Brogle (1983) McBride (1984)
Alsec R.	1.3, 1.2	1981–83	McBride and Brogle (1983), McBride (1984)
Situk R.	1.3, 1.2, 2.2, 2.3	1966, 1968, 1971, 1974–79, 1981, 1983 escapements	Mc Bride and Brogle (1983), McBride (1984)
Copper R.	1.3, 1.2	1982, 1983	Sharr 1983, Sharr et al. (1985)
Central Alaska			
Susitna	1.3, 1.2	1972–81	Cross et al. (1983)
Kenai	1.3, 1.2, 2.2, 2.3	1972–81	Cross et al. (1983)
Kasilof	1.3, 1.2, 2.2	1972–81	Cross et al. (1983)
Karluk	2.2, 2.3, 3.2	1922, 1924–49	Rounsefell (1958)
Chignik R. (Chignik L.)	2.3, 2.2		Various FRI and ADF&G reports
Chignik R. (Black L.)	1.3, 2.3, 1.2		Various FRI and ADF&G reports
Western Alaska			
Kvichak R.	2.2, 1.2, 1.3, 2.3	14 yr	Various ADF&G Tech. Data Reports and Bristol Bay annual Management Reports
Naknek R.	2.2, 1.3, 2.3, 1.2	14 yr	
Wood R.	1.2, 1.3, 2.2	14 yr	
Nuyakuk R.	1.3, 1.2, 2.2	14 yr	
Igushik R.	1.3, 1.2, 2.2, 2.3	14 yr	
Egegik R.	2.2, 2.3, 1.3, 1.2	18 yr	
Ugashik R.	2.2, 1.2, 1.3, 2.3	18 yr	
Togiak R.	1.3, 1.2, 2.2	18 yr	
Kuskokwim R.	1.3, 2.3, 1.2	1982–83	Huttunen (1984b, 1985)
Kanektok R.	1.3, 1.2	1982–83	Huttunen (1984b, 1985)
Goodnews R.	1.3, 1.2	1982–83	Huttunen (1984b, 1985)

TABLE 2. The most common age-groups of sockeye salmon, by river system. (Underline indicates age-group is always predominant. Inclusion of an age-group indicates it has exceeded 20% in one or more of years examined). (*Continued.*)

River system or stock	Age-groups	Remarks	Source
Kamchatka			
Ozernaya R.	2.3, 2.2, 3.2, 3.3	1940-59	Egorova et al. (1961)
Bolshaya R.	1.3, 1.2, 1.4	1935-47	Semko (1954)
Kamchatka R.	1.3, 2.3	1957-60	Hanamura (1966)
Lake Dalnee	1.2, 2.2, 1.3	1934-43	Krogius and Krokhin (1948)

ducing lakes than in others. This reflects in larger size of juvenile sockeye in food-rich lakes unless controlled by higher densities of sockeye and competitors. In a comparison of zooplankton biomass, sockeye growth rates and sockeye biomass in Owikeno, Babine–Nilkitkwa, and Dalnee lakes, Brocksen et al. (1970) concluded that higher rates of food production should lead to higher food densities and these to higher consumer (juvenile sockeye) growth rates and biomasses. In this example, Lake Owikeno had the lowest zooplankton biomass per m^3, Babine–Nilkitkwa, intermediate, and Lake Dalnee, many-fold higher, which is reflected in the great differences in mean smolt size shown in Table 1.

The growth potential available to individual sockeye is evident in newly stocked lakes when sockeye biomasses are still at low levels. Growth rate of juvenile sockeye in Frazer Lake remained very high until recent years, when as spawning escapements and smolt output increased, mean smolt size decreased (Blackett 1984). Lake Washington sockeye also exhibit high growth rates. In this situation, the biomass of zooplankton is high and planktivores (primarily juvenile sockeye) crop less than 2% of the annual zooplankton production (Eggers et al. 1978). Lake Washington represents an extreme case, compared to most other sockeye systems, in that the growing season is long, zooplankton standing crop is very high, and sockeye growth is very good.

The growth potential for individual sockeye is also measurable in lakes at times when population biomass is low because of historically low or reduced parent spawning levels and competition among progeny is at a minimum. The growth history of juvenile sockeye in the main lake basin of Babine Lake provides an example. This nursery area was underutilized because of the historically limited capacity of adjacent spawning grounds (Johnson 1956, 1958, 1961). Following up on this conclusion, the Canadian government built artificial spawning channels that increased fry output nearly threefold. This resulted in roughly equivalent increases in the abundance of underyearlings and smolts (McDonald and Hume 1984). For several years after this nearly threefold increase in average abundance, no significant change in the mean size of smolts was noted. Thus during the period that the zooplankton supply in Babine Lake was underutilized, yearling sockeye smolts still averaged only about 5 g in weight, as compared to 18.5 g in Lake Washington and over 50 g in Frazer Lake in initial years after sockeye introductions.

It has been demonstrated for several oligotrophic sockeye lakes that the addition of nutrients, usually some combination of ammonium phosphate and ammonium nitrate, has increased the production of phytoplankton and zooplankton and the growth rate of juvenile sockeye (see for example Nelson 1959; Rogers 1979; Hyatt and Stockner 1985). Several investigators have also studied the relative contribution of phosphorus released from the carcasses of sockeye salmon in the phosphorus budget of sockeye lakes (for example Rounsefell 1958; Donaldson 1967; Krokhin 1967; Koenings and Burkett 1987 a). The potential change in lake nutrient levels resulting from long term decline in escapement levels with intensification of fishing rates has been of particular concern. Changes in Lake Dalnee, east Kamchatka, suggest such an occurrence.

Lake Dalnee, the smallest of the lakes with high spawner density, is only $^1/_{56}$ the area of Lake Kuril, the major Kamchatkan sockeye lake. Sockeye production in Lake Dalnee has been studied intensively by Soviet scientists since the 1930's. Spawner densities averaged 169 fish/ha of rearing area over the period 1937–68, but escapements declined precipitously over this period, from an average of 402 spawners/ha in the first 10 yr to 34/ha in the last 10 yr. Paradoxically, in spite of the sharp drop in parent population density, yearling sockeye length also declined, from an average of 9.1 cm for 1938–47 broods to 8.0 cm for 1956–65 broods (Krogius 1972, table 4). The decline in smolt size apparently is a consequence of decline in escapement level, since Krokhin (1967) found a declining phosphate component in Lake Dalnee which he attributed to the declining number of spawning salmon over the period 1937–60. Decline in Karluk sockeye escapement may have had a similar effect on lake productivity and smolt size in Karluk Lake (see smolt size change, Table 1, and discussion by Koenings and Burkett 1987a).

PHYSICAL CONDITIONS

Physical conditions affecting growth potential in sockeye lakes include (1) water temperature and thermal stratification, (2) photoperiod and length of growing season, and (3) turbidity and available light in the water column.

Lake temperature and temperature stratification affects the diel and seasonal feeding behavior and depth preferences of juvenile sockeye in different lake environments. Feeding experiments over a range of constant temperatures revealed that young, small sockeye show a sharp growth optimum at 15°C and that growth conversion efficiency (% flesh from food) peaks at a lower temperature, 11.5°C (Brett 1971). Still lower temperatures suppress conversion efficiency, growth rate, maximum meal size, and digestion rate. During the annual periods of lake temperature stratification, juvenile sockeye undergo diel vertical migrations which are influenced by conditions of food supply, light and temperature in the various lakes (Narver 1970; Brett 1971; Woodey 1972; McDonald 1973; Eggers 1978; Levy 1987). Feeding strategies are modified to adapt to ambient conditions.

In Lake Iliamna, Bristol Bay, annual growth of juvenile sockeye is greatly influenced by water temperature. Rogers and Poe (1984) found that whether juveniles from a given brood year migrate at age 1, or age 2, is primarily deter-

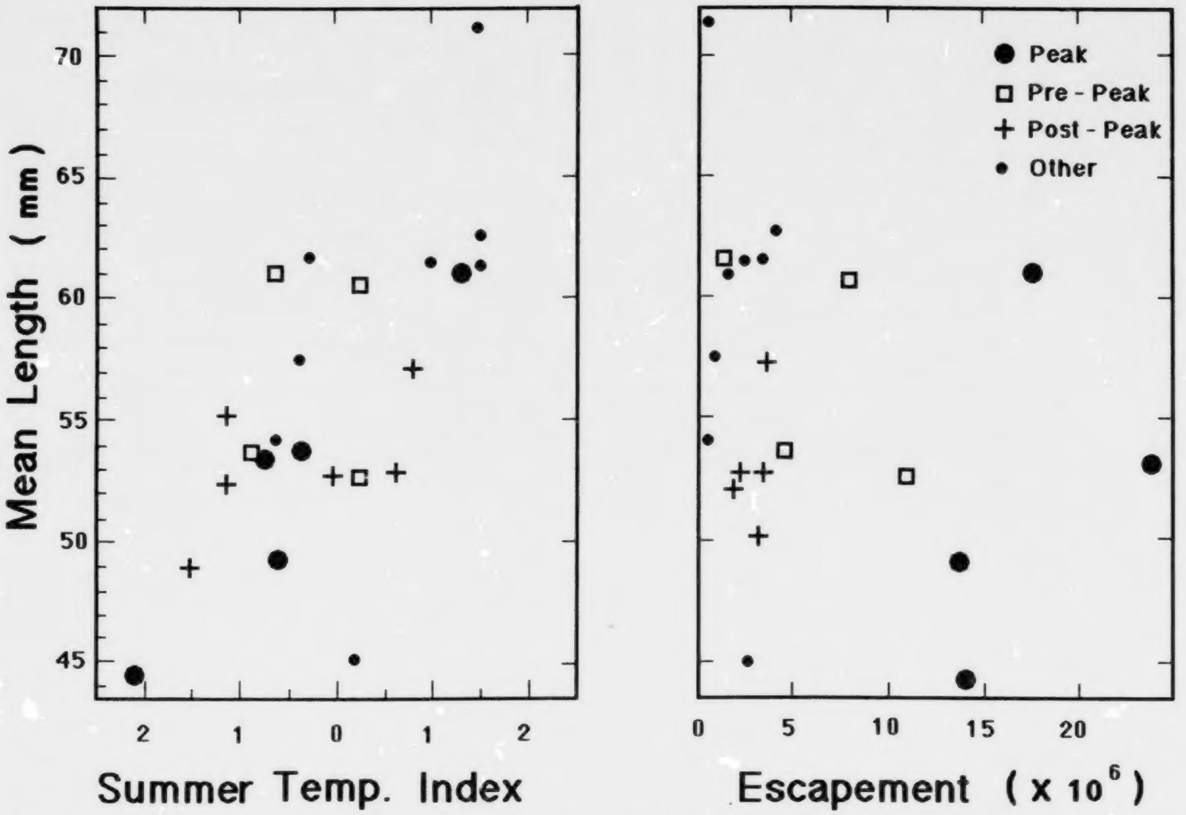

FIG. 1. Mean length of sockeye fry in Lake Iliamna on September 1 of each year plotted against summer temperature index (left graph) and against parent escapement (right graph). Relation of year to cycle is indicated on graph. (After Rogers and Poe 1984, fig. 20).

mined by the weather from spring through fall (for the fry), and secondly by the weather in the following spring (when they would smoltify as age 1.). The annual growth of fry in Lake Iliamna, as estimated by their mean length on September 1, was more closely related to water temperature than to the size of the parent escapement, which varies greatly during the course of the run cycle (Fig. 1). In Lake Aleknagik, Bristol Bay, a significant part of the annual variation in length of sockeye salmon fry in the littoral zone at the beginning of summer is explained by surface water temperatures (Rogers 1973). Since water temperature in late June is largely a function of the date of ice breakup and amount of solar radiation, the growth attained in the spring by sockeye fry is primarily a function of climatological conditions. The early season influence of climatic conditions is also apparent in the amount of new summer growth appearing on scales of yearling smolts (Burgner 1962a). Differences between years in amount of new growth attained by a given calendar date during early summer was related to time of breakup of lake ice and lake temperatures subsequent to breakup. In Chilko Lake, British Columbia, a deep, cold lake at high elevation with a short growing season, temperature during fry emergence and early lake residence accounted for much of the recorded fluctuation in freshwater growth as indicated by circulus counts on the scales of returning adult salmon (Goodlad et al. 1974).

The effect of length of growing season is illustrated by comparison of seasonal growth trajectories between juvenile sockeye populations in Lake Washington and Lake Aleknagik in Bristol Bay (Fig. 2). The period of rapid size increase begins about 2$^1/_2$ months later in Lake Aleknagik, and, not shown, ends earlier in the autumn, since surface water temperatures in the lake usually drop below 4°C by the end of October (Rogers 1979).

A number of sockeye lakes are turbid from glacial runoff, interfering with light penetration in the water column and resulting in shallower euphotic zones for phytoplankton production (Ruggles 1966; Koenings and Burkett 1987b). Examples are Owikeno Lake in coastal British Columbia, Tustumena and Kenai lakes in Cook Inlet. Growth of juvenile sockeye in these lakes is slow, at least partially because of lower zooplankton production. The juvenile sockeye, being visual feeders, must feed in near-surface waters. In other lakes, organic colloids discolor the water and reduce light penetration, again reducing the volume of the epilimnion available for photosynthesis (Koenings et al. 1985). (See Koenings and Burkett 1987b, for more in-depth discussion of the influence of euphotic zone depth on lake productive capacity.)

Competition

Competition for common food or space resources during lake residence may exist in years when numbers of juvenile sockeye in a year-class are large, when there are two or more year-classes utilizing the same resources, or when other species are also utilizing the resources. In the strict sense, competition exists only if the resources are in short supply,

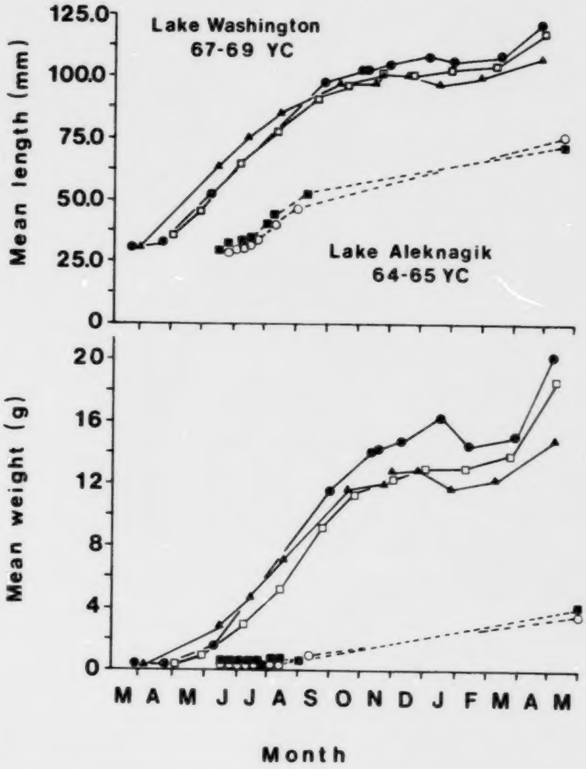

FIG. 2. Seasonal growth trajectories of length and weight of underyearling sockeye for Lake Washington (1967–69 year-classes) and Lake Aleknagik (1964–65 year-classes). (After Eggers 1978, fig. 6.)

or if not in short supply, the fish seeking the resource nevertheless harm one another in the process (Birch 1957). If food is in short supply the juvenile sockeye or their competitors or both may grow more slowly.

INTRASPECIFIC COMPETITION

If the nursery area food supplies limit the population of juvenile sockeye that the lake will support, then progeny of large spawning populations may show evidence of reduced growth. This is evident in some of the Bristol Bay and Fraser River lakes.

Summer growths exhibited by underyearling sockeye in the Wood River lakes, Bristol Bay, provide the first example. The five main lakes of the Wood River system are similar in nursery area quality (water chemistry, primary production, zooplankton standing crop/unit lake area) and over a period of years have had nearly the same average abundance of spawning salmon/km^2 of lake area (Burgner 1964; Burgner et al. 1969). However, in individual years the spawning population balance among lakes may be quite uneven, and differences in the growth of progeny have then become apparent (Burgner 1962a). From 1958 on, annual samples of young salmon for growth studies have been collected with pelagial tow nets within each lake (Rogers et al. 1980). Results of the sampling show the distinct inverse relationship between numbers of parent spawners per unit nursery lake area and mean weight of progeny toward the end of their first summer in the lake (Fig. 3).

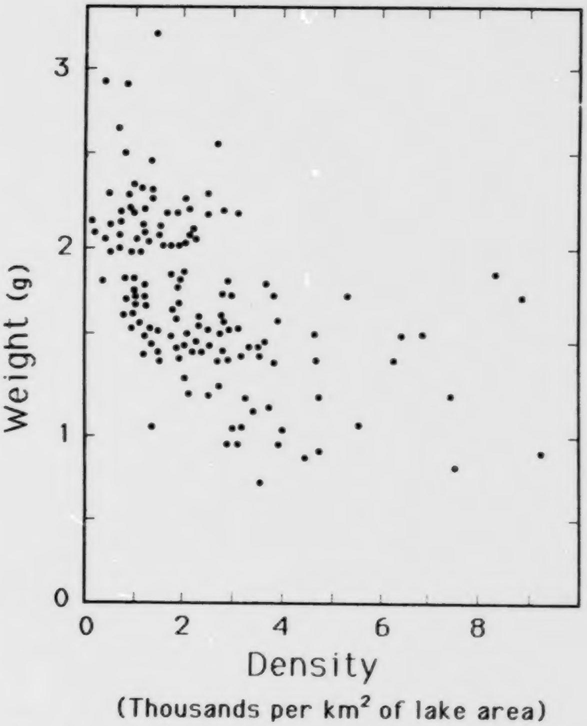

FIG. 3. Mean weights of underyearling sockeye salmon on 1 September (1958–79) in each of the Wood River lakes vs. the relative density of parent spawners (prior year). (After Rogers et al. 1980, fig. 11).

This effect of density on growth carries over to time of smolt migration. Mean weights of age 1. and 2. smolts from both the Wood and Kvichak rivers were inversely related to the density of parent spawners (Fig. 4). Wood River smolts are mostly age 1. fish and are typically the smallest smolts in Bristol Bay. Population densities of sockeye range higher in the Wood and Kvichak systems than in lakes of the Naknek and Ugashik systems, where density dependent growth is not as obvious (Fig. 5).

Reduced growth is also apparent at higher sockeye population densities in some Fraser River lakes. Goodlad et al. (1974) used parent spawners (in this case, females/ha) as an index of population density of fry produced and used the freshwater scale circulus count of returning adult salmon as a growth index to examine density-growth relations for 20 annual spawning runs to each of four lakes (Fig. 6). The inverse relationship between density and growth was significant at the 1% level in Shuswap and Cultus lakes, and at the 5% level in Fraser Lake. The relationship in Chilko Lake, with the shortest growing season, was not significant, perhaps because of the greater influence of climate on growth.

In the Naknek lake system of Bristol Bay, Ellis (1974) concluded that growths of juvenile sockeye and potential competitor species were not related to abundance of these fish in any lake of the system. There was no apparent reduction in growth in areas of higher densities of juvenile salmon. Coville Lake, at the upper end of the system, received in some years as much as 65% of the spawning escapement in the Naknek system but has only 3% of the available rearing area (Hartman and Burgner 1972). The potential for growth

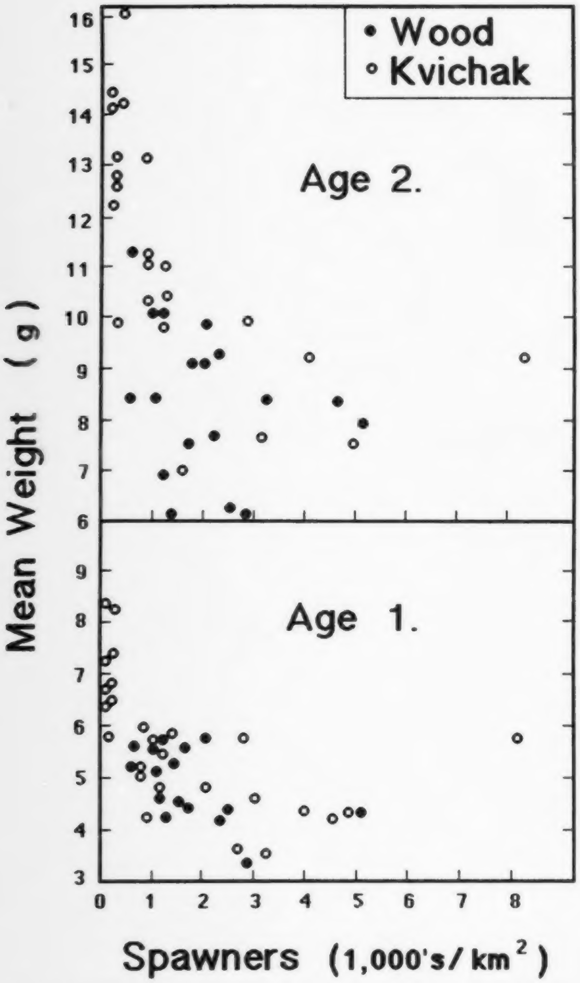

FIG. 4. Plots of the mean weight of smolts on the relative density of parent spawners (number per km^2 of lake area) in the Wood River and Iliamna–Clark lake systems. (After Rogers 1980, fig. 2).

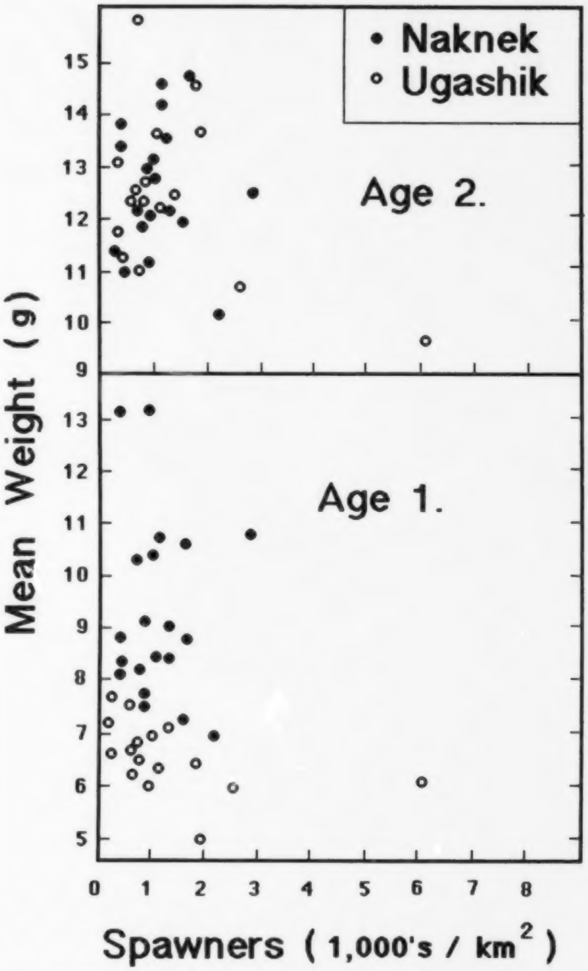

FIG. 5. Plots of the mean weight of smolts on the relative density of parent spawners (number per km^2 of lake area) in the Naknek and Ugashik lake systems. (After Rogers 1980, fig. 3).

reduction in Coville Lake was reduced by summer interlake migration of a portion of the fry out of Coville Lake into Grosvenor and Naknek lakes, where population densities were much lower. In the Naknek system, two of the major basins were deemed to have insufficient fry input, because of lack of adequate spawning area in one case and underutilization of spawning areas in the other.

In Bristol Bay and Fraser River lake systems, juvenile growth limitations are apparent at spawner densities above 20/ha of lake rearing area. However average spawner densities several times greater are seen in Karluk, Kuril, Dalnee, and Chignik lakes (Table 3). It is therefore of interest to examine growth of juveniles in two of these systems.

During 1921–36, spawner densities in Karluk Lake averaged a phenomenal 282 fish/ha and reached 634/ha. In spite of these high densities and the fact that most of the resultant juveniles held over to age 2. or 3. to smoltify, growth achieved by yearling and age 2. smolts was considerably better than that in Bristol Bay populations (Table 1). Rounsefell (1958) found no apparent density effect on growth and concluded that the runs during this period were not sufficiently large for the juveniles to deplete the available food supply; i.e., that biomass in the lake did not adversely affect growth. Interestingly, juvenile coho salmon (*Oncorhynchus kisutch*), like juvenile sockeye, also have, in spite of good growth, an extended period of residence in Karluk Lake, smoltifying primarily at ages 2. and 3. (Drucker 1972).

Lake Kuril, the productive caulderal lake on the southeast tip of Kamchatka Peninsula, provides a second instance of high spawner density. Lake Kuril spawner densities have been high historically, averaging 199 fish/ha of rearing area for the period 1940–65 and reaching 553/ha in 1949. As in Karluk, the predominant smolt age is age 2., with age 3. second in abundance. However, Lake Kuril smolts are much smaller at a given age than Karluk smolts and are also smaller than Bristol Bay smolts (Table 1). According to Selifonov (1970) the young of the year (age 0) do not move offshore into the deep parts of the lake until September–November and thus do not compete with the age I and age II fish until then. The latter two age-groups are mixed during the entire season, but the percentage holding over to smoltify at age 3. is low. Annual differences in growth rate were associated

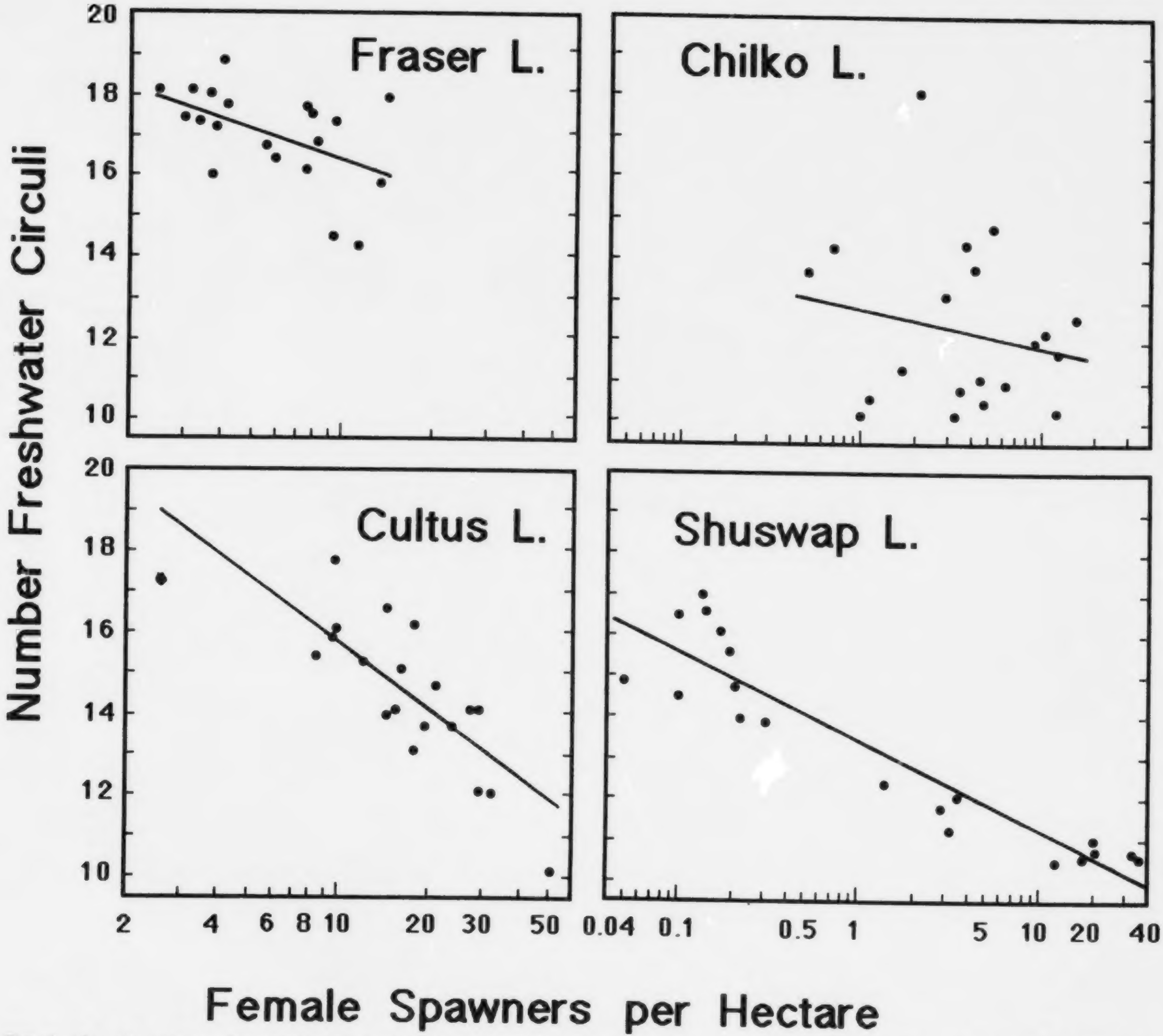

FIG. 6. Female spawners/ha of lake area and freshwater scale growth of offspring for 20 yr of spawning runs (1949–68) at Cultus, Chilko, Fraser, and Shuswap lakes. (After Goodlad et al. 1974, fig. 5).

both with the numerical strength of contiguous year-classes in the lake as well as lake water temperature (Selifonov 1970). While extremely low growth was observed under the combined strain of overpopulation and poor environmental conditions, the young sockeye grew at an accelerated pace when low numbers and favorable environmental conditions prevailed. Selifonov stated it was difficult to say which factor (population size or climate) dominated when they had opposing influences on growth. Competitors are apparently few in number and interspecific competition is of no significance in Lake Kuril.

INTERSPECIFIC COMPETITION

Interspecific competition implies an interaction between juvenile sockeye and other fish species that affects natality, survival, and /or individual growth rate in one or both species. If food is in short supply the juvenile sockeye or their competitors or both may grow more slowly. Interactive segregation may also occur, in which the interaction between two species forces them to magnify their differences in habitat or food selection (Nilsson 1965).

Several non-salmonid species overlap with the juvenile sockeye in their lake distribution and food habits, and the fish communities and relative abundance of species vary from lake to lake. Species with food habits overlapping those of juvenile sockeye include threespine and ninespine sticklebacks, (*Gasterosteus aculeatus* and *Pungitius pungitius*), pond smelt (*Hypomesus olidus*), and pygmy whitefish (*Prosopium coulteri*). Lake whitefish (*Coregonus clupeaformis*), abundant in Morrison Lake, B.C., were reported to feed pelagically on the same plankters as young sockeye and to be a potential competitor (McMahon 1948). Overall, the threespine stickleback is the most abundant species associated with juvenile sockeye salmon in the Wood River, Kvichak, Naknek, Chignik and Karluk systems (Burgner et al. 1969), Lake Nunavaugaluk (Jaenicke et al. 1987), the Igushik system (Rogers and Newcome 1975), the

TABLE 3. Comparisons of numbers of sockeye spawners per hectare of available lake rearing area in Pacific rim sockeye lake systems.

Lake or lake system	Lake area (ha)	Spawning years	Spawning escapement (mean and range) 1000's	Spawners/ha (mean and range)
Washington State				
Washington	8 760	1970–82	299(107–435)	26(12–50)
Fraser River				
Cultus	627	1949–72	19(3–56)	30(5–89)
Chilko	20 030	1949–72	199(19–596)	10(1–30)
Fraser	5 460	1949–72	62(25–141)	11(5–26)
Shuswap	30 960	1949–72	451(3–2 120	15(1–68)
Coastal B.C.				
Sproat	4 100	1970–82	68(25–215)	17(6–52)
Great Central	5 085	1970–82	136(15–253)	27(3–50)
Long	2 300	1970–82	99(21–214)	43(9–93)
Owikeno	9 600	1970–82	433(102–985)	45(11–103)
Babine	49 600	1946–82	668(102–888)	13(2–18)
Alaska				
Karluk	4 000	1921–53	902(400–2 533)	226(100–633)
		1954–83	342(138–590)	86(35–148)
Chignik	6 100	1965–84	690(470–905)	113(77–148)
Iliamna-Clark	288 900	1964–83	6 300(227–24 326)	22(1–84)
Naknek	79 000	1964–83	1 136(357–2 665)	14(5–34)
Becharof	113 200	1964–83	834(329–1 445)	7(3–13)
Ugashik	38 500	1964–83	682(39–3 321)	18(1–86)
Wood R.	42 500	1964–83	1 119(330–2 969)	26(8–70)
Igushik	7 400	1964–83	383(60–1 988)	51(8–269)
Nuyakuk	27 900	1964–83	426(20–3 027)	15(1–108)
Kamchatka				
Kuril	7 600	1940–65	1 512(300–4 200)	199(39–553)
Dalnee	136	1937–68	23(1–100)	169(7–735)
Blizhnee	350	1938–60	36(4–83)	103(11–237)

Nuyakuk system (Burgner, unpublished), as well as in several other Alaska lakes studied. Threespine sticklebacks were slightly less abundant than ninespine sticklebacks in Chignik Lake but were much more abundant in nearby Black Lake. Pond smelt are sometimes locally abundant, e.g., in Coville Lake of the Naknek system and the Chignik Lakes and are the most abundant potential competitor in Lake Azabache, in the lower Kamchatka River basin (Krogius and Krokhin 1956a). Pygmy whitefish, which are basically benthic, were highly abundant in trawl catches from Brooks Lake of the Naknek system (Burgner et al. 1969). In Lake Dalnee, east Kamchatka, ninespine stickleback occurred in large numbers in the littoral areas, while threespine stickleback were mainly in the limnetic area (Krogius and Krokhin 1948). Neither sticklebacks nor any other serious competitor of young sockeye were found in Babine Lake, B.C., (Withler et al. 1949). For 15 other sockeye lakes on Vancouver Island and the Mainland coast of British Columbia, sampling indicated that only Alastair had a dense population of threespine stickleback in the pelagic zone while lakes Nimpkish and Owikeno had lower population densities (Simpson et al. 1981). Threespine sticklebacks were observed to be the second most abundant fish in 17 lakes of coastal British Columbia, but consistently occupied the limnetic zone during the summer growing season in only about half of these lakes (Hyatt and Stockner 1985). In the Fraser River system, no potential competitors of significance were reported by Goodlad et al. (1974) in the pelagic zones of Chilko, Shuswap, Fraser, and Cultus lakes.

In Great Central Lake considerable dietary overlap was observed between threespine stickleback and sockeye juveniles sampled together in littoral areas in May–July (Manzer 1976). It was noted, however, that during the year the two species occur together only in the littoral zone, and that sockeye salmon are found almost entirely in the limnetic zone. Therefore it was inferred that because of the different distribution patterns of the two species, they are not serious competitors for food in Great Central Lake despite their similarity in diet.

In the Wood River lakes the size of the combined populations of juvenile sockeye and threespine sticklebacks affected feeding, and thus growth of both populations (Rogers 1968, 1973). An increased abundance of sockeye salmon fry resulted in decreased growth of both species in early summer. In the littoral zone of lower Lake Aleknagik, the diets of both species consisted predominantly of midges, although the sockeye fed more heavily on adult forms. In the limnetic zone the diets of both species consisted largely of entomostracans, but again, winged insects were important in the diet of sockeye and nearly absent from the diet of stickleback. Although annual variation in the relative abundance of the non-salmonid species did not appear to affect the growth of juvenile sockeye, there presumably was competition for food.

A reported feature in Lake Dalnee, Kamchatka, is the complex interaction of sticklebacks as competitor and buffer species to juvenile sockeye (Krogius and Krokhin 1956a). Despite a relatively high plankton content in the lake and generally high growth rates for young sockeye, extensive intra- and interspecific competition was reported to have reduced their growth rate in some years and sometimes caused them to remain in the lake for a second or even a third year. Unusually large numbers of threespine sticklebacks competing for the same planktonic food was given as the chief reason for the very low numbers of seaward-migrant sockeye in three years (Krogius and Krokhin 1956b), although the mechanism of mortality was not reported. Markovtsev (1972) found a high similarity in food habits of the two species in the pelagic area of the lake during certain months of the year. Dolly Varden char (*Salvelinus malma*) were thought to benefit young sockeye by destroying competing sticklebacks (threespine and ninespine). Sticklebacks were the dominant food of Dolly Varden during early summer (Savvaitova and Reshetnikov 1961), while juvenile sockeye were a minor food item. Hanamura (1966) concluded that a higher abundance of sticklebacks in Lake Dalnee reduces the Dolly Varden predation on sockeye but increases the amount of competition for food between sticklebacks and sockeye.

Interactions between juvenile sockeye and resident species have also been studied in Black Lake of the Chignik Lake system, Alaska Peninsula. Narver (1966) and Dahlberg (1968) concluded that low allocations of parent spawning escapements in past years was responsible for underutilization of the Black Lake nursery area. This was believed to have resulted in an increase in the abundance of resident fishes in Black Lake which could compete with the juvenile sockeye for food and space, and sockeye escapements were subsequently adjusted by Alaska Department of Fish and Game in an attempt to provide a more appropriate balance. A follow-up study of interactions between juvenile sockeye and resident species was therefore conducted (Parr 1972). In shallow Black Lake it was found that abundance of resident fishes apparently did not affect growth of sockeye underyearlings. The summer diets of sockeye, threespine and ninespine sticklebacks, and pond smelt overlap but differ in substantial ways — i.e., the sticklebacks depend heavily on aquatic insect larvae, the pond smelt on Cladocera and copepods, and the sockeye primarily on adult insects, to a lesser extent on zooplankton, and to a minor extent on insect larvae. However there was a strong inverse relationship between the initial year-class strength of young sockeye in early summer and that of both threespine and ninespine sticklebacks. Apparently the age 0 sticklebacks were less able to survive in the presence of large numbers of age 0 sockeye, which enter the lake before the young sticklebacks hatch. There was no evidence that the young sockeye were feeding to any extent on stickleback eggs or larvae. At any rate, tow net sampling results supported the initial hypothesis: with increased escapement and more sockeye juveniles, the abundance of competitor species in Black Lake declined.

Behavior and Genetic Influences

Numerous observed instances of differences in behavior among populations of juvenile sockeye suggest genetic adaptations which have resulted in improved survival and growth. Following are a few brief examples concerning feeding behavior in lakes.

1. Directional migration of emergent fry. Miller and Brannon (1981) noted that the sockeye is the only salmon in which the young are known to undergo genetically directed migrations from their natal streams, and that fry emerging from redds in each spawning area exhibit unique directional or rheotactic preferences that enable them to reach their nursery lake. Several investigators have documented these behavioral differences among populations of sockeye fry.

2. Use of littoral area. In some populations, sockeye fry move directly into the limnetic zone to feed shortly after emergence. This is exemplified by fry emerging from Cultus Lake beaches (Brannon 1972) and from the Cedar River into Lake Washington (Woodey 1972). In other populations, pronounced sequential feeding in littoral areas within the lake occurs for several weeks, as in the Wood River Lakes (Burgner 1962b; Rogers 1968; Pella 1968) and in Lake Dalnee (Krogius and Krokhin 1956a). The extreme occurs in Lake Kuril, where the underyearlings occupy the littoral zone for most of their first growing season (Selifonov 1970).

3. Diel vertical migrations. (See discussion by Levy 1987). Although characteristics of the complex diel vertical migrations of feeding juvenile sockeye differ considerably among populations in contrasting lake environments, it is not known to what extent these differences in behavior among populations are genetically controlled.

4. Summer interlake migration. As previously noted, summer interlake migration of underyearling progeny in the Naknek Lake system occurs from a lake of high spawning density into a lake of low spawning density. As in the Naknek system, summer interlake migration of underyearling sockeye occurs between Black Lake (upper lake) and Chignik Lake (lower lake). This is in contrast to underyearling behavior in the Wood River system, where spawning density among lakes is more uniform and interlake migration of fry has not been detected (Hartman and Burgner 1972). On the average in this system it would appear advantageous for underyearlings in the upper lakes to remain in their home lake to feed than to risk contributing to a more congested feeding environment in a lower lake in the system.

5. Age at seaward migration. The lack of a consistent relationship among populations between growth rate and average age at seaward migration suggests that the survival advantage of migrating early (at age 1.) vs migrating at an older age (2. or 3.) must have differed among lake populations historically, resulting in genetically controlled tendencies for age at smoltification. For example, sockeye population densities in Lake Becharof are the lowest of the major Bristol Bay lake systems (Table 3), and smolt size at a given age is the largest. In spite of their good growth, a much higher proportion of juveniles remain an extra year in Becharof Lake to smoltify at age 2. Little is known of the relative abundance of competitor or predator populations in the lake, but this delayed migration behavior suggests that in this lake there is an overall survival advantage in staying longer in fresh water. Incidentally, the sockeye run to Lake Becharof has exhibited more stability in numbers than populations of other Bristol Bay lake systems.

Discussion and Conclusions

In this review paper I have discussed some factors possibly contributing to the complex array of age and growth combinations among juvenile sockeye in lakes around the North Pacific. Evidence is also presented which implicates the external effects of lake environment, climate, interspecific competition, and predation. However, there are strong examples of intraspecific competition, as well as evidence of genetically controlled differences among juvenile populations in behavior and age at seaward migration that influence freshwater growth and survival.

Within lakes, the usual factors examined for indications of population pressure are changes in sockeye growth rate and age at seaward migration. However such changes are also seen to result from annual differences in climatic conditions. Many juvenile sockeye populations show no evidence of population density effects on growth or age at seaward migration, while others clearly do.

Although competitors may exert and influence on sockeye growth and production in some nursery lakes, juvenile sockeye greatly predominate in most feeding areas, particularly in the limnetic zones of the larger lakes. Therefore, when indications of competition are evident, they are likely to be predominantly intraspecific. Differences in spatial distribution and in food habits between juvenile sockeye and potential competitors contribute to reduce interspecific competition, and interactive segregation is quite likely in some cases.

Among lakes there are large differences in juvenile growth rate and in age composition of seaward migrants. While fast-growing fish tend to smoltify at an earlier age, age at seaward migration quite obviously has a racial, or genetic, component apparently related to historical conditions for success in the nursery lake and the ocean. Other behavioral adaptations for effective utilization of individual nursery areas include directional migration of emergent fry, differential use of littoral and pelagic areas, differences in diel vertical migrations, and differences in interlake migration tendencies.

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An Experimental Study of Competition for Food Between Sockeye Salmon (*Oncorhynchus nerka*) and Threespine Sticklebacks (*Gasterosteus aculeatus*) in a British Columbia Coastal Lake

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Abstract

O'NEILL, S. M., AND K. D. HYATT. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake, p. 143–160. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Evidence supporting the hypothesis that competitive interactions occur between juvenile sockeye salmon and limnetic sticklebacks in oligotrophic lakes was obtained by manipulating abundance, size and species combinations of fish in enclosures in the limnetic zone of Kennedy Lake, British Columbia. Sockeye and sticklebacks were stocked at densities within the range known to commonly occur in British Columbia coastal lakes. In all enclosures containing fish, fish grazing pressure quickly reduced the abundance of large zooplankters and then maintained zooplankton communities containing primarily nauplii and rotifers, prey seldom consumed by fish. Mean size and abundance of zooplankton within a fishless control enclosure remained at significantly higher levels than those in Kennedy Lake or in test enclosures. We conclude that in many oligotrophic coastal lakes, where food supplies are limited, sockeye and sticklebacks compete by exploiting the zooplankton communities to their mutual disadvantage.

Résumé

O'NEILL, S. M., AND K. D. HYATT. 1987. An experimental study of competition for food between sockeye salmon (*Oncorhynchus nerka*) and threespine sticklebacks (*Gasterosteus aculeatus*) in a British Columbia coastal lake, p. 143–160. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Par manipulation de l'abondance, de la taille et des espèces de poissons gardés dans des enclos de la zone limnétique du lac Kennedy (Colombie-Britannique), les auteurs ont recueilli des preuves qui étayent l'hypothèse que des interactions compétitives ont lieu entre le saumon nerka juvénile et l'épinoche limnicole peuplant les lacs oligotrophes. Des saumons nerkas et des épinoches ont été gardés à des densités de la gamme communément observée dans les lacs côtiers de la Colombie-Britannique. Dans tous les enclos à poissons, le broutage a rapidement réduit l'abondance du gros zooplankton tandis que les communautés zooplanctoniques composées surtout de larves nauplii et de rotifères, des proies rarement consommées par le poisson, sont restées à un niveau stable. Dans un enclos sans poisson, la taille moyenne et l'abondance du zooplankton sont demeurées à des niveaux nettement plus élevés que ceux notés dans le lac Kennedy ou dans les enclos expérimentaux. Les auteurs formulent la conclusion que dans plusieurs lacs côtiers oligotrophes où l'apport en nutriments est limité, le saumon nerka et l'épinoche se font concurrence en exploitant les communautés zooplanktoniques à leur désavantage mutuel.

Introduction

Numerous investigations have demonstrated an inverse relationship between the abundance of juvenile sockeye salmon (*Oncorhynchus nerka*) per unit area in lakes and their rates of growth (Burgner 1962; Mathisen and Kerns 1964; Ruggles 1965; Johnson 1965; Rogers 1973; Goodlad et al. 1974). In an analysis of density-dependent aspects of trophic processes, Brocksen et al. (1970) reported an inverse relationship between the biomass of young sockeye and the biomass of their food from several widely distributed oligotrophic lakes. Evidence from these studies, as well as others (Brett 1971, 1983), persuades us that the growth rate, and possibly survival (LeBrasseur et al. 1978) of young sockeye are food-limited within a wide range of nursery lakes. Given this condition, competition for limited food resources has generally been regarded as an important process influencing the production of sockeye salmon in lakes.

In many lakes juvenile sockeye are the most numerous limnetic fish species (Foerster 1968; Hartman and Burgner 1972; Rogers 1973), thus intraspecific competition has usually been considered to play the major, if not exclusive, role in controlling juvenile sockeye production (Burgner 1987). Although often suggested as potentially important, evidence that interspecific competition for food influences sockeye production is largely circumstantial (e.g. Krogius and Krokhin

1956a; Hartman and Burgner 1972) or negative (Rogers 1973). In a recent study of 17 lakes along the British Columbia coast, Hyatt and Stockner (1985) conducted nutrient addition experiments which demonstrated that juvenile sockeye growth was both food-limited and strongly influenced by variations in the abundance of all limnetic fish. Since threespine sticklebacks (*Gasterosteus aculeatus*) were numerically dominant in the limnetic zones of approximately half of the lakes studied, interspecific competition between juvenile sockeye and limnetic sticklebacks could exert considerable influence over sockeye production in many nursery lakes.

Sticklebacks may compete with sockeye directly by removing food items that would be consumed by sockeye (exploitative competition), or indirectly by altering the amount of food available to sockeye via overt or subtle behavioural interactions (interference competition). In this study we provide further insight into the mechanisms mediating competitive interactions between sockeye and sticklebacks by manipulating abundance, size, and species combinations of fish in experimental enclosures maintained in the limnetic zone of Kennedy Lake, British Columbia. Zooplankton communities subject to fish predation are examined to ascertain if sockeye and sticklebacks exploitatively influence the size and species composition of the food resource.

Materials and Methods

STUDY SITE

This study was carried out at Kennedy Lake (49°06′N, 125°33′W) located on the west coast of Vancouver Island, British Columbia (Fig. 1). The lake is 4 m above sea level, 6 475 ha in area and has a mean depth of 38 m (Rutherford et al. 1986). It has two major arms (Main and Clayoquot) connected by a narrow (100 m) channel through which there appears to be very little exchange of either nutrients or fish (K. D. Hyatt, unpublished data). In common with the majority of warm monomictic lakes of the outer British Columbia coast, Kennedy Lake is characterized by a short water residence time (1.1 yr), low phosphorus concentration (1.2–2.0 µg TP • L^{-1} in an untreated state), and extremely oligotrophic conditions (1.08–2.01 µg TChl • L^{-1} untreated) (Stockner and Shortreed 1985). The major basins

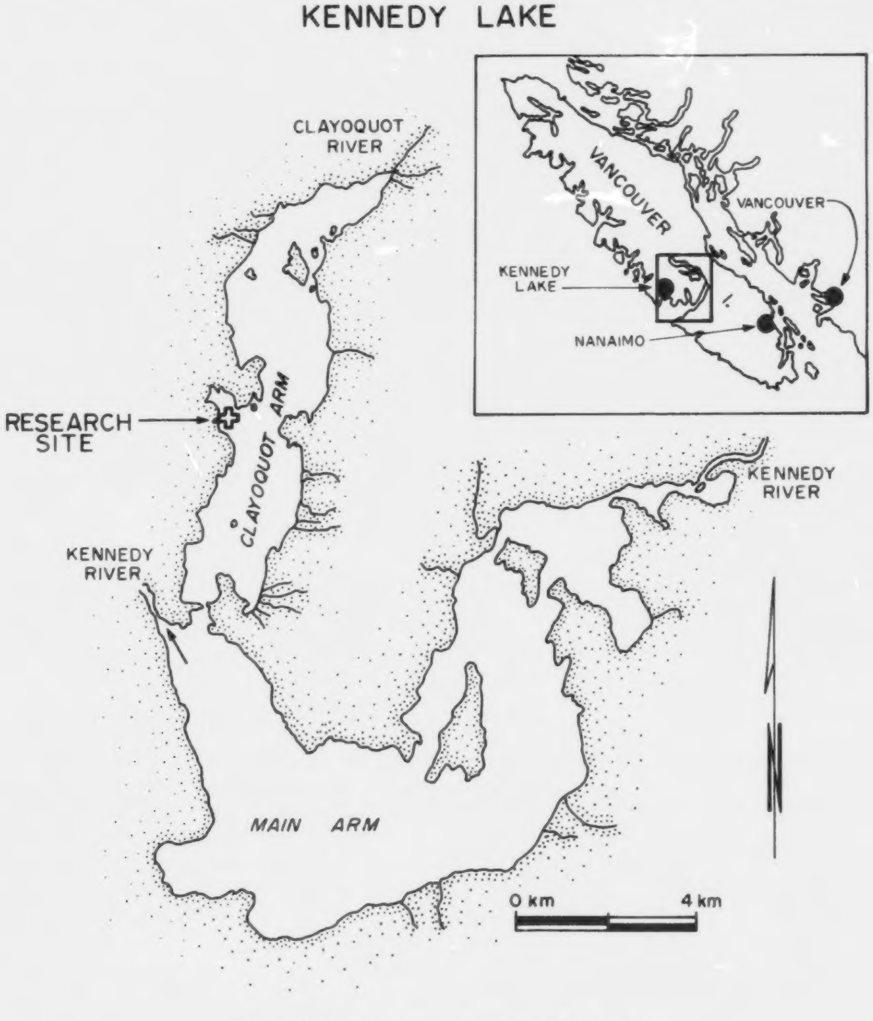

FIG. 1. Kennedy Lake, Vancouver Island, B.C.

of the lake are deep, and littoral zone habitat (< 5 m depth) is restricted to approximately 3.2% of the lake's surface area. Combinations of beach seining, minnow trapping, mid-water trawling, and echo sounding, have been used to assess the fish populations (Hyatt et al. 1984). In decreasing order of abundance, the fish species known to occupy the lake are: threespine sticklebacks, sockeye salmon, prickly sculpin (*Cottus asper*), peamouth chub (*Mylocheilus caurinus*), cutthroat trout (*Salmo clarki clarki*), and coho salmon (*O. kisutch*). The limnetic fish population of the lake is relatively simple; juvenile sockeye and sticklebacks are the only fish which regularly occupy offshore waters of the lake to exploit zooplankton as a major food source.

The limnetic zooplankton community is also simple. The small cladoceran, *Bosmina coregoni longispina* (Deevey and Deevey) is very abundant whereas the larger cladocerans (*Diaphonosoma* sp., *Sida* sp., and *Polyphemus* sp.) are rare. *Daphnia* spp. appear to be absent from the lake. Cyclopoid copepods (*Diacyclops thomasi* and rarely *Cyclops vernalis*, Fisher) are more numerous than calanoid copepods (*Diaptomus oregonensis* (Lilljeborg) and *Diaptomus kenai* (Fisher). *Keratella* sp. and *Kelicottia* sp. are rotifers which regularly achieve high seasonal abundance. *Neomysis mercedis*, a mysid, is the largest zooplankter routinely sampled in the limnetic zooplankton community (K. D. Hyatt, unpublished data).

Both arms of the lake have been treated with inorganic nutrients at various times since 1978 as part of a Lake Enrichment Program (Hyatt and Stockner 1985) and studies are underway to determine the responses of both target (juvenile sockeye) and non-target species to lake fertilization. The experiments discussed below were conducted in Clayoquot Arm in 1983. The lake was fertilized in 1983, but there is no reason to suspect this would affect the results to be reported here.

ENCLOSURE EXPERIMENTS

Numerous investigators have documented that planktivorous fish are size-selective predators (see reviews in Hall et al. 1976; Mills and Schiavone 1982). Fish predation influences both the species and size composition of zooplankton communities directly, by removing the large herbivores, or indirectly, by removing the large predaceous zooplankters that consume the smaller herbivorous zooplankters. Consequently, the size and species composition of zooplankton communities are shifted towards smaller mean body sizes in environments containing planktivorous fish. Theoretical as well as empirical evidence suggest that reductions in the mean body size of zooplankton will frequently reduce the scope for growth in populations of planktivorous fish in general (Mills and Schiavone 1982) and sockeye in particular (Eggers 1977, 1982). Consequently, we concluded that examinations of the relative effects of planktivorous sockeye and sticklebacks on the structure of zooplankton communities in field enclosures could be used to test the hypothesis that direct food removal is one mechanism that controls interspecific competition between the two fish species.

To test whether limnetic sockeye and sticklebacks influence the zooplankton community to their mutual disadvantage and thereby compete exploitatively, it is necessary to examine the zooplankton communities and fish diets for each fish species separately and together in similar environments. In

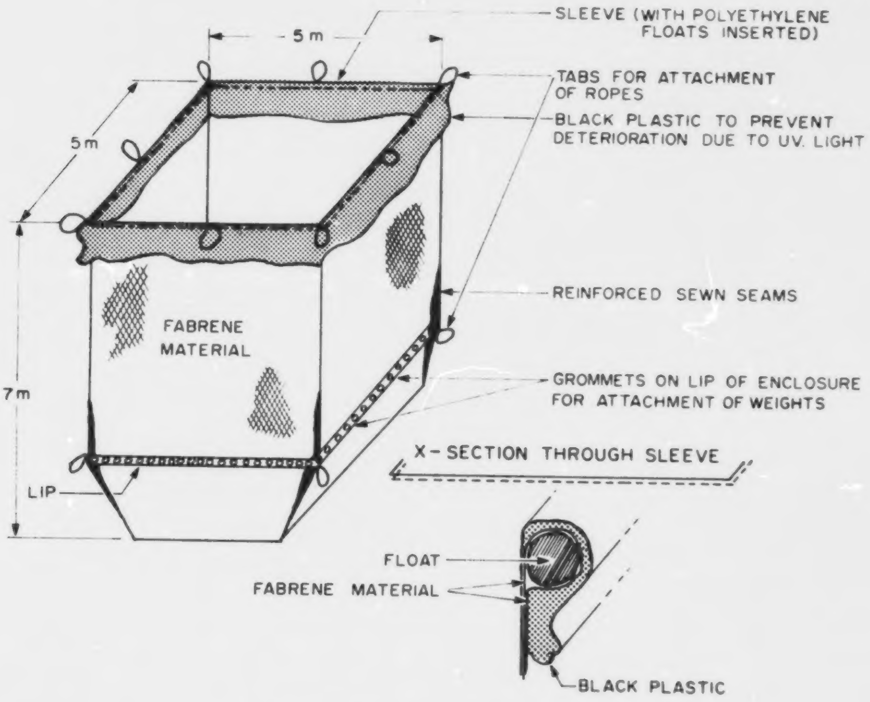
SLEEVE (WITH POLYETHYLENE FLOATS INSERTED)
5 m
5 m
TABS FOR ATTACHMENT OF ROPES
BLACK PLASTIC TO PREVENT DETERIORATION DUE TO UV. LIGHT
REINFORCED SEWN SEAMS
FABRENE MATERIAL
7 m
GROMMETS ON LIP OF ENCLOSURE FOR ATTACHMENT OF WEIGHTS
X-SECTION THROUGH SLEEVE
LIP
FLOAT
FABRENE MATERIAL
BLACK PLASTIC

FIG. 2. Diagram of experimental enclosure.

situ enclosures were chosen as the test apparatus as fish could be separated for study yet allowed access to similar food supplies.

Experiments were conducted in 5 × 5 × 7 m polyethylene enclosures (Fig. 2; see O'Neill 1986 for details). These were small enough to avoid patchiness of zooplankton distribution yet large enough to avoid strong "edge effects" (Stephenson et al. 1984). Enclosures were suspended from the lake's surface by flotation collars and anchored in a protected cove of Kennedy Lake (Fig. 1). The bottoms of the enclosures were 2–4 m above the lake bottom.

EXPERIMENTAL DESIGN AND PROCEDURES

Experiments were designed to test the hypothesis that single species populations of sockeye and sticklebacks (allopatric treatments) would have the same impact on the size and species composition of zooplankton communities as mixed species populations (sympatric treatments). Evidence supporting this hypothesis would suggest that in the limnetic zone of lakes, sockeye and sticklebacks are trophic analogues that compete whenever food supplies are limiting. Connell (1983) has pointed out that many experimental studies of competition support only weak inferences about the role of competition in natural environments because the experiments are not representative of the spatial and temporal variations that natural populations and environments commonly exhibit. Therefore, we adopted guidelines suggested by Connell and repeated the same basic competition experiment in each of spring, early summer and fall of 1983. Heating of the epilimnion and water stratification precluded conducting experiments during mid-summer when surface temperatures were high enough (21–26°C) to adversely affect juvenile sockeye. The physiologically optimum temperature for sockeye is 15°C (Brett 1971) and the summer thermocline occurs at depths normally exceeding those of our experimental enclosures. Experimental trials conducted during each of the 3 time periods utilized the sizes and developmental stages of sockeye and sticklebacks most readily available then. Hereafter, results presented from each of these time periods and involving unique combinations of fish size classes, dominating each species population in the lake (Table 1), will be referred to as either Experiment 1, Experiment 2, or Experiment 3.

In each experiment a "replacement series" treatment design (de Wit 1960) was used in which the total density of fish in the enclosures was kept constant regardless of species composition. The sockeye to stickleback ratios used in treatments within each experiment were 1:0, 1:1, and 0:1. The 1:1 sympatric treatment was replicated to provide equal sample sizes of fish for statistical analysis. A fishless control enclosure was maintained during each experiment for a total of five enclosures and four treatments (Table 1). In each experiment, comparisons were made of the species and size composition of zooplankton in the enclosures before and after introductions of fish.

Fish were collected from the lake by using a midwater trawl (Gjernes 1979) and kept in a holding pen for 2 days. Healthy fish were then removed, weighed or measured, and stocked into enclosures. The density of fish in the enclosures was approximately twice the density in Kennedy Lake in 1983 (2 700 smolts or 5 400 fry • ha^{-1}, see Table 1) but within the range of densities observed in other years (K. D. Hyatt, unpublished data). The day after fish introductions, enclosures were inspected by SCUBA divers and dead fish (approximately 10%) were replaced with similar sizes of the appropriate species. Fish were allowed to feed for a period of about 2–3 wk in enclosure trials.

At approximately weekly intervals, integrated 7 m vertical plankton samples were collected with the aid of a cable and pulley mechanism that enabled sampling from the centre of each enclosure. A conical black net (mouth dimensions 0.25 m^2, 100 μm mesh) was used to collect the samples. Samples were used to compare the effects of the different fish treatments on the zooplankton communities. Because the lake contained a lower fish density than the fish treatment enclosures (Table 1), its zooplankton community served as an intermediate comparison between fish treatments and the fishless control enclosure.

TABLE 1. Size (fork length of sockeye and standard length of sticklebacks) and numbers of fish used in enclosure experiments.

			No. of fish per enclosure			
Experimental group (and mean size)	Date (1983)	Stocking density (fish • ha^{-1})	Allopatric sockeye	Allopatric sticklebacks	Sympatric replicate 1	Sympatric replicate 2
Experiment 1						
Sockeye yearlings ($\bar{x}$ = 64 mm)	April 15–27	4 000	10 sockeye	10 sticklebacks	5 sockeye +	5 sockeye +
Adult sticklebacks ($\bar{x}$ = 52 mm)					5 sticklebacks	5 sticklebacks
Experiment 2						
Underyearling sockeye ($\bar{x}$ = 51 mm)	October 10–30	4 000	10 sockeye	10 sticklebacks	5 sockeye +	5 sockeye +
Juvenile sticklebacks ($\bar{x}$ = 38 mm)					5 sticklebacks	5 sticklebacks
Experiment 3						
Sockeye fry ($\bar{x}$ = 28 mm)	May 7–26	9 600	24 sockeye	24 sticklebacks	12 sockeye +	12 sockeye +
Juvenile sticklebacks ($\bar{x}$ = 33 mm)					12 sticklebacks	12 sticklebacks

Plankton samples were preserved in a sucrose-buffered, 4% formalin solution (Haney and Hall 1973) for later analysis. Plankton samples were subsampled according to the guidelines of Edmondson (1971) and McCauley (1984). All zooplankton within a subsample were identified to genus or species and total body length (length excluding spines, antennae and setae) was measured with the aid of an electronic caliper-microcomputer arrangement (Sprules et al. 1981). A portion of the remaining sample was scanned for large or rare zooplankters. The total number of zooplankters per cubic meter was calculated for both subsample (less the large and rare zooplankters) and scan observations, and then summed. Because the net sampled only approximately 1% of the enclosure volume, sampling probably did not alter the zooplankton community. Replicate haul contents were very similar (O'Neill 1986) thus a single haul was considered to be representative of the zooplankton within the enclosures.

At the end of each experiment, fish were removed from the enclosures and preserved for gut content analysis. Fish were fixed in 10% buffered formalin for at least 1 wk after which they were transferred to 50% ethanol for 1 wk. Finally, the fish were preserved in 95% ethanol for at least 5 wk after which they were weighed and measured (total length of sticklebacks and fork length of sockeye). Stomachs were removed and prey items were identified and then measured with an electronic caliper. When prey items were broken or digested, undigested hard body parts were used to estimate the total lengths of the prey. Total body lengths of chironomid larvae were estimated from the length and width of the heads (see O'Neill 1986 for conversions). In all but five of the stomachs, the total contents were identified and enumerated, thus minimizing subsampling errors associated with gut content analysis.

Enclosures used in Experiment 2 and Experiment 3 had been previously subjected to experimental manipulations (e.g. yearling sockeye and adult stickleback additions), and accordingly their zooplankton communities differed from that of Kennedy Lake. Between experiments, zooplankton were collected from the lake, mixed thoroughly, and then added to the fish-treatment enclosures in large enough quantities to re-establish similar zooplankton communities.

Heavy wave activity during storms in early May caused corners of some of the enclosures to tear thereby permitting the entry of fish from the lake. To effectively remedy invasions by fish into the enclosures, corners of the enclosures were mended and all fish were removed by SCUBA divers or through use of a seine net. Additionally, the fishless control enclosure was surrounded by an outer barrier of 1/4" nylon mesh netting which precluded further entry by fish throughout the experiments even in the event of additional tears developing in the enclosure.

DATA ANALYSIS

Net efficiency appears to be relatively constant within seasons (K.D. Hyatt, unpublished data) and therefore observations of zooplankton abundance in samples were not adjusted for variation in net efficiency. A Kolmogorov-Smirnov two-sample test (Siegel 1956; hereafter referred to as K–S test) was used to determine if size frequency distributions of zooplankton decreased significantly between the start and finish of a given experiment. A Kruskal-Wallis nonparametric analysis of variance (ANOVA) was used to test whether mean zooplankton sizes among treatments were different at the start and end of the experiment. For start and end samples, body length measurements from individual zooplankters in samples collected from the various treatments were ranked by increasing size and analyzed with a single factor (i.e. treatment) ANOVA. (A single factor ANOVA applied to ranked data approximates a Kruskal–Wallis test; SAS Statistical Package, 1985.) Tukey's multiple comparison of means test was used to determine homogeneous sets of ranked means among the treatments.

Results

Across the time interval of the three experiments, zooplankton mean size, abundance of all species of zooplankton (i.e., total abundance) and number of adult copepods were substantially greater in the enclosure maintained without fish than in the lake, except when the enclosure was torn and fish invaded (Fig. 3). Although absolute numerical differences were large, qualitatively similar seasonal trends in total abundance appear to have taken place in the lake and the fishless enclosure, validating the use of enclosures to create allopatric and sympatric environments that are qualitatively similar to the lake.

EXPERIMENT 1. SOCKEYE YEARLINGS AND ADULT STICKLEBACKS (APRIL 15–27)

Fish were initially excluded from all enclosures for 12 days to confirm that enclosures would prevent both entry and exit of fish. Prior to introductions of fish at the start of Experiment 1, all enclosures contained zooplankton communities of similar species and size compositions. The copepod *D. thomasi* was the dominant zooplankter, followed by nauplii or *B. coregoni*, and rotifers (Fig. 4a, c, e, 5a). The same taxa were present in the lake samples; however, nauplii were numerically dominant over *D. thomasi* (Fig. 5c). Zooplankton size in all enclosures was uniformly high (range of means 0.44 to 0.56 mm; Fig. 6a, c, e, 7a), although there were statistically significant differences in the mean sizes of zooplankton from enclosure and lake samples (Kruskal–Wallis test; Table 2a). Zooplankters sampled from the lake (Fig. 7c) were significantly smaller (Tukey's procedure; Table 2a) than those from the enclosures (Mean size 0.34 mm vs. 0.51 mm, respectively). Total numbers of zooplankton varied among enclosure and lake samples from a low of $5\ 564 \bullet m^{-3}$ to a high of $17\ 277 \bullet m^{-3}$ (Fig. 4, 5).

Experiment 1 was terminated approximately 2 wk after the introduction of fish (sockeye mean length = 64 mm, stickleback mean length = 52 mm) into four of the enclosures. Comparisons of zooplankton communities among enclosure and lake samples between the start and end of the experiment indicated substantial changes had occurred to the species, size and total numbers of zooplankton. Many, but not all, of these changes appeared to be a direct outcome of differences in the relative intensity of fish grazing on the zooplankton communities.

In all enclosures containing fish, nauplii and rotifers replaced *D. thomasi* as the dominant zooplankter (Fig. 4b, d, f). However, few changes in taxa occurred in either the fishless control, where *D. thomasi* and *B. coregoni* continued to

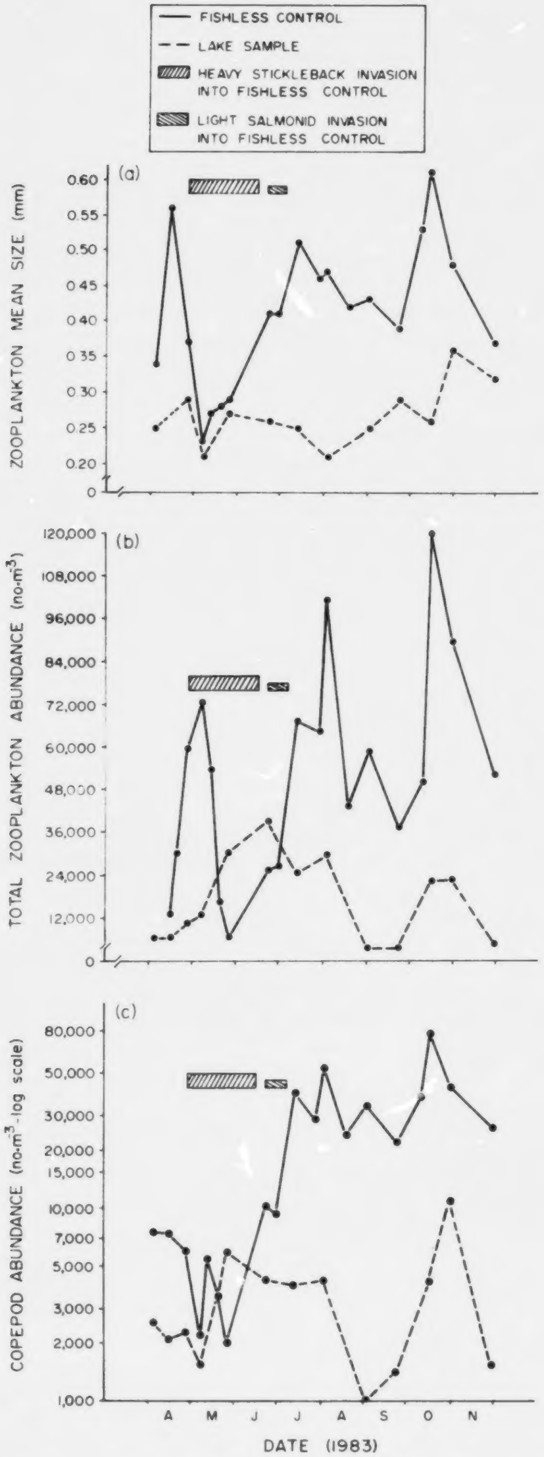

FIG. 3. Temporal comparison of zooplankton mean size, total abundance and copepod abundance in a fishless enclosure and in Kennedy Lake. (Heavy stickleback invasion consisted of 24 fish entering from April 27 to June 16. Light invasion consisted of 1 salmonid entering from June 23 to July 7.)

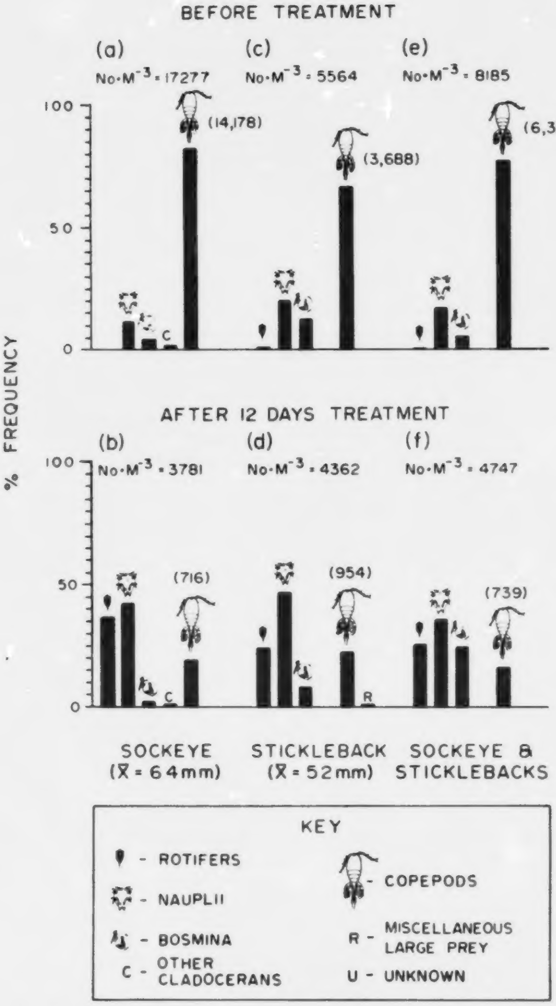

FIG. 4. Frequency distributions (as %) of zooplankton by taxa in enclosures before (a, c, e) and after (b, d, f) treatment with allopatric and sympatric groupings of sockeye yearlings and adult sticklebacks. (*Two replicates from sympatric treatments have been pooled.)

dominate the zooplankton community (Fig. 5b), or in the lake, where nauplii remained dominant (Fig. 5d), as at the start of the experiment. The size composition of zooplankton among experimental treatments shifted in accord with the species changes. All fish treatment enclosures contained significantly higher proportions of small zooplankton at the end of the experiment than at the start (K-S df=2, $\chi^2=418.42$, 130.42, 340.00, and 12.21; $P<0.001$ for all fish treatments) and the range of mean sizes of zooplankton decreased from 0.45–0.56 mm to 0.19–0.25 mm (Fig. 6). Indeed, although the ranked mean sizes of zooplankton >0.35 mm exhibited significant differences among fish treatment enclosures prior to the start of Experiment 1, these differences were not significant by its end (Tukey's procedure; Table 2a). This suggests that sockeye and stickleback predation tended to drive somewhat different zooplankton communities towards a common end point.

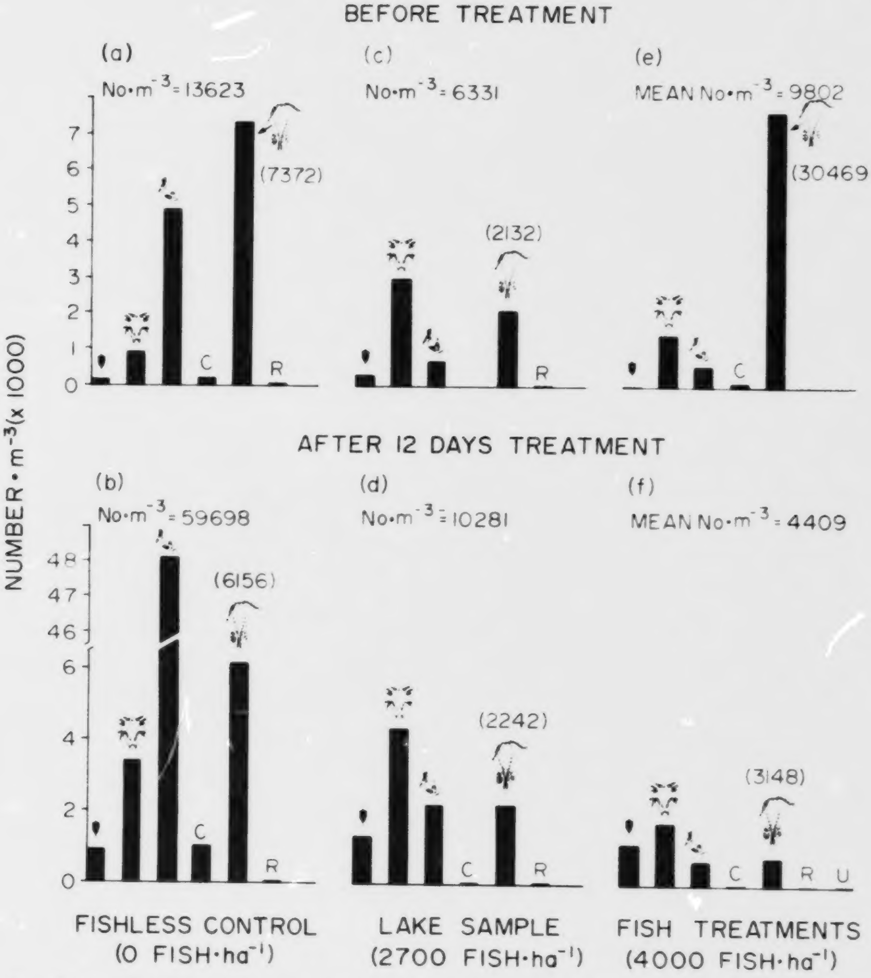

FIG. 5. Comparison of frequency distributions of zooplankton by taxa sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of sockeye yearlings and adult sticklebacks (e, f).

A number of comparisons of pooled results from the fish treatments with results from the fishless control and lake-sample "control" suggest that fish predation, rather than any other factor, was the main determinant of changes in zooplankton communities within the enclosures. By the end of Experiment 1, the mean sizes of zooplankton from both the fishless control and the lake were significantly larger (Tukey's procedures; Table 2a) than those from the fish treatments. Further, by the end of the experiment, higher fish densities among treatments (i.e., fishless control < lake < fish treatments; Table 1) were associated with zooplankton communities characterized by successively smaller mean body size (0.37, 0.29 and 0.22 mm, respectively) and successively lower total numbers (59 698; 10 281 and 4 409•m^{-3}, respectively, Fig. 5).

Zooplankton, size decreases were not just a simple consequence of removal of large zooplankton from enclosures by fish since zooplankton size decreased significantly not only in fish treatment enclosures but also in the fishless control (K–S test, df=2, $\chi^2 = 110.08$, $P < 0.001$) and in the lake (K–S, df=2, $\chi^2 = 14.19$, $P < 0.001$). It appears that size decreases were a complicated outcome of zooplankton species and abundance changes that differed among the lake, the fishless control, and the fish treatments. In both the fishless control and in the lake, moderate shifts to smaller zooplankton (mean size from 0.56 to 0.37 mm and from 0.34 to 0.29 mm, respectively) were achieved through disproportionate increases in the numbers of *B. coregoni* (compare Fig. 5a&b, c&d) which accompanied increases in the absolute abundance of all zooplankton taxa (from 13 623 to 59 698 and from 6 331 to 10 281 animals•m^{-3}, respectively; Fig. 5). By contrast, in all enclosures containing fish, much greater decreases in zooplankton size were achieved (range of means from 0.45–0.56 mm to 0.19–0.25 mm) through disproportionate decreases in the abundance of *D. thomasi* and *B. coregoni* which accompanied dramatic decreases in the total abundance of zooplankton (from a mean of 9 802 to 4 409 animals•m^{-3}; Fig. 5e, f). In enclosures with fish, only rotifers and nauplii, in size groups seldom exploited by fish (see fish diet analysis below), exhibited numerical increases by the end of the experiment.

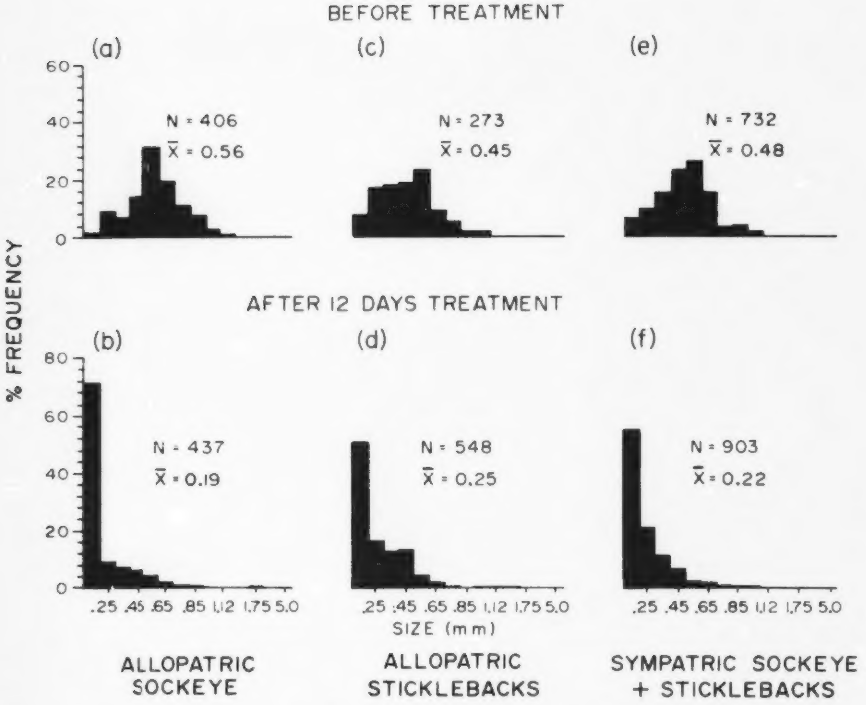

FIG. 6. Frequency distributions (as %) of zooplankton by size in enclosures before (a, c, e) and after treatment (b, d, f) with allopatric and sympatric groupings of sockeye yearlings and adult sticklebacks. (*Two replicates from sympatric treatments have been pooled.)

TABLE 2. Results of nonparametric ANOVA on zooplankton sizes from experiments with (a) sockeye yearlings and adult sticklebacks, (b) underyearling sockeye and (c) sockeye and stickleback fry. For each experiment, treatments are listed in descending order of ranked mean zooplankton size. Replicate treatments are indicated by numbers in parentheses. Treatments exhibiting homogeneous sets of means are bracketed.

Experiment	Sampling time: Start	Sampling time: Finish
(a)	(F = 120.32, df = 5, $P<0.0001$)	(F = 13.61, df = 5, $P<0.0001$)
	Sockeye	Lake sample
Sockeye yearlings and	Fishless control	Fishless control
Adult Sticklebacks	Sockeye and Sticklebacks(1)	Sockeye
	Sticklebacks	Sockeye and Sticklebacks (2)
	Sockeye and Sticklebacks (2)	Sockeye and Sticklebacks (1)
	Lake sample	Sticklebacks
(b)	(F = 67.19, df = 5, $P<0.0001$)	(F = 77.98, df = 5, $P<0.001$)
Underyearling	Fishless control	Fishless control
Sockeye and	Sockeye and Sticklebacks (2)	Lake sample
Sticklebacks	Sockeye	Sticklebacks
	Lake sample	Sockeye
	Sockeye and Sticklebacks (1)	Sockeye and Sticklebacks (2)
	Sticklebacks	Sockeye and Sticklebacks (1)
(c)	(F = 13.89, df = 4, $P<0.0001$)	(F = 7.15, df = 3, $P<0.0001$)
Sockeye and	Sockeye	Lake sample
Sticklebacks fry	Sockeye and sticklebacks	Sockeye and Sticklebacks (2)
(Replicate 2 of	Lake sample	Sockeye
sympatric treatment	Sticklebacks	Sticklebacks
and fishless control	Fishless control	
excluded due		
to fish invasion)		

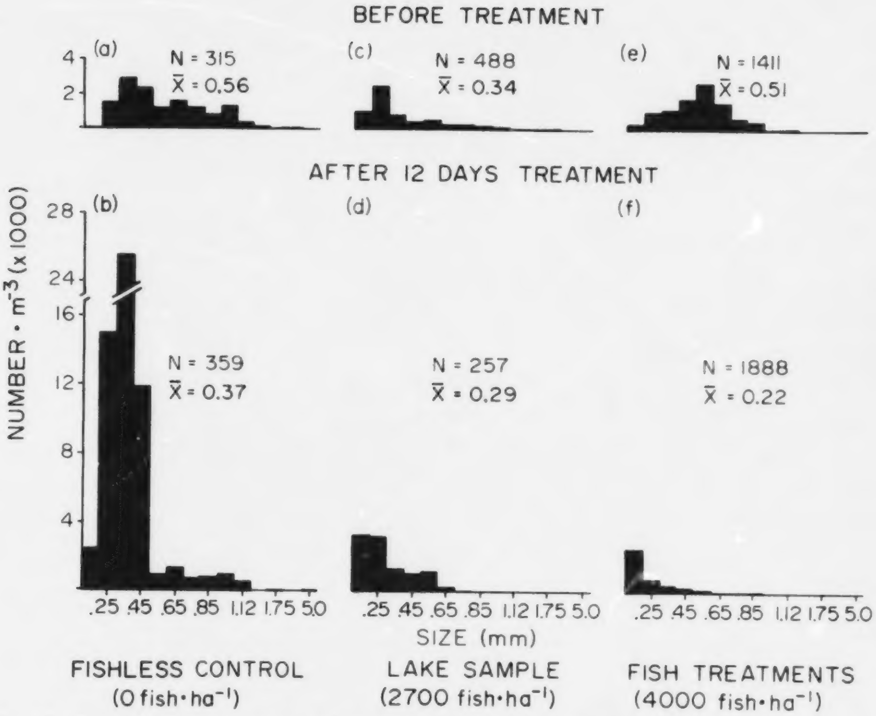

FIG. 7. Comparison of frequency distributions of zooplankton by size sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of sockeye yearlings and adult sticklebacks (e, f).

EXPERIMENT 2. UNDERYEARLING SOCKEYE AND JUVENILE STICKLEBACKS (OCTOBER 10–30)

Prior to the start of Experiment 2, significant differences (Tukey's Procedure, Table 2b) existed among zooplankton communities present in the experimental enclosures and the lake due principally to the differences in treatments applied to enclosures during Experiment 1. The control enclosure, which had been fishless since early June, contained significantly larger mean sizes of zooplankters than the other enclosures and the lake (Tukey's Procedure – Table 2b). It also supported a higher abundance of zooplankton, and contained mostly large *Diacyclops* (Fig. 8a). The enclosures which had contained fish during Experiment 1 had zooplankton which were similar in size and, in all but one of the enclosures (replicate 2 of the sympatric treatments), nauplii were the numerically dominant zooplankter followed by the copepod *Diacyclops* (Fig. 9a, c, e). Replicate 2 of the sympatric treatment was more like the lake sample as *B. coregoni* and nauplii dominated its zooplankton community. Regardless, at the start of Experiment 2, the mean sizes of zooplankton in all four enclosures previously exposed to fish treatment were similar to each other and to the lake sample (0.25–0.33 mm range of means) but very different from the fishless enclosure (0.53 mm, see Fig. 10a, c, e, 11a).

By the end of Experiment 2, three of the four enclosures that had contained underyearling sockeye (mean length = 51 mm) and sticklebacks (mean length = 38 mm) for 20 days, displayed significant shifts to smaller zooplankton (K–S, df=2, χ^2=44.10, 29.31 and 35.57; $P<0.001$ for all treatments, Fig. 10b&f). The allopatric stickleback enclosure (Fig. 10c&d) was the exception as the zooplankton size-frequency distribution did not shift to include significantly more small zooplankton (K–S, df=2, $\chi^2=1.729$, $P>0.05$). However, even in this enclosure, the proportion of zooplankters greater than 0.5 mm did decline significantly between the start and finish of the experiment (difference between proportions test, Zar 1974, df=∞, $Z = 2.1059, 0.05 > P > 0.02$). The shift to smaller zooplankters in the fish treatment enclosures was less dramatic here than in Experiment 1 but resulted from a similar phenomenon: disproportionate loss of the large copepods (average 39% decline, Fig. 9b, d, f). Slight to moderate changes in total zooplankton abundance were noted in all three enclosures containing fish (Fig. 9).

Within the fishless control enclosure, zooplankton sizes decreased only slightly, although significantly (K–S, df=2, $P<0.001$), between the start (mean size 0.53) and end (mean size 0.49 mm) of the experiment (Fig. 11a&b). Unlike the fish treatment enclosures, the zooplankton size decrease was due to a disproportionate increase in the number of *Bosmina*, and not a decrease in absolute copepod abundance (copepods increased 10%). During the time covered by Experiment 2, the size of zooplankton in the lake did not decline significantly (K–S, df=2, $\chi^2=0$, $P>0.05$). However, there was a shift in taxonomic composition from *B. coregoni* to *Diacyclops*. Absolute copepod abundance in the lake increased by 190% (Fig. 8c&d).

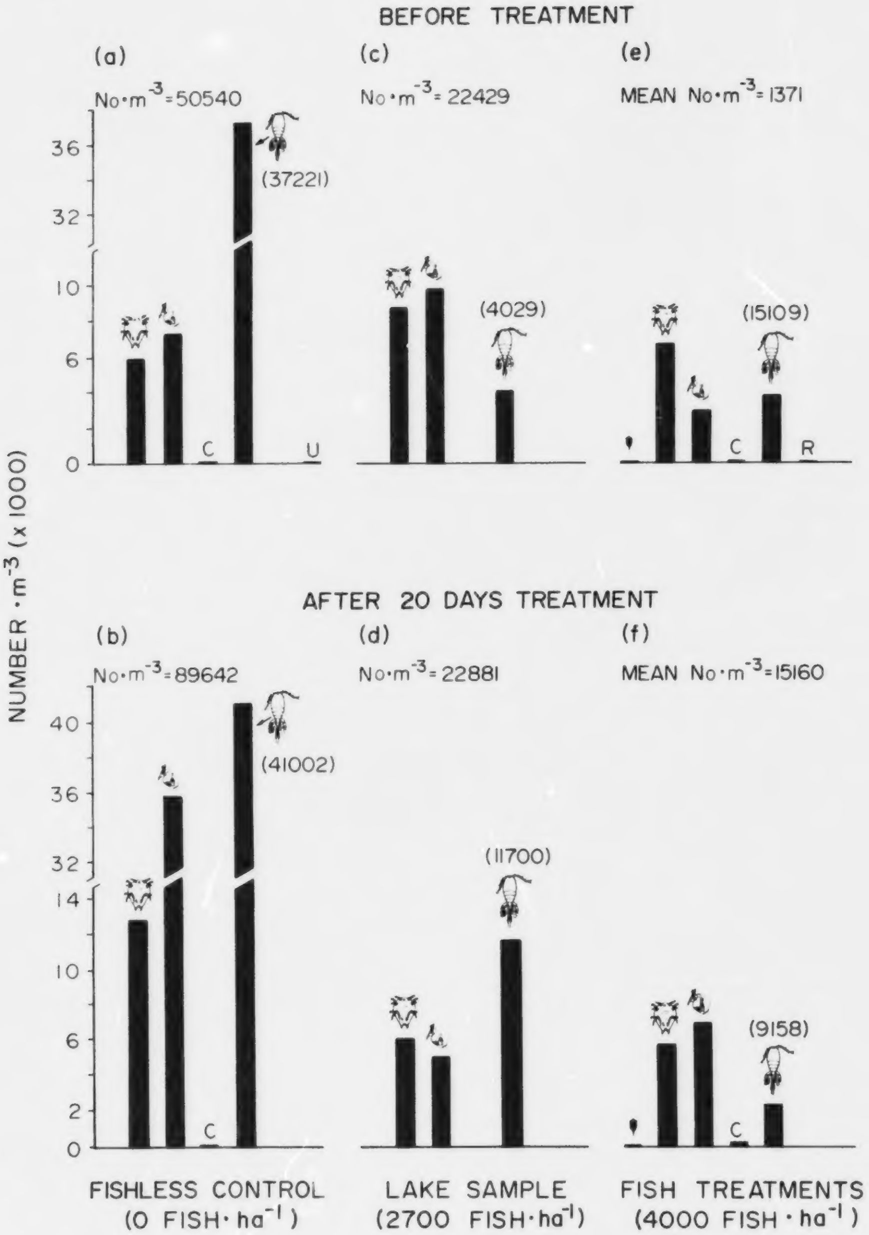

FIG. 8. Comparison of frequency distributions of zooplankton by taxa sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of underyearling sockeye and juvenile sticklebacks (e, f).

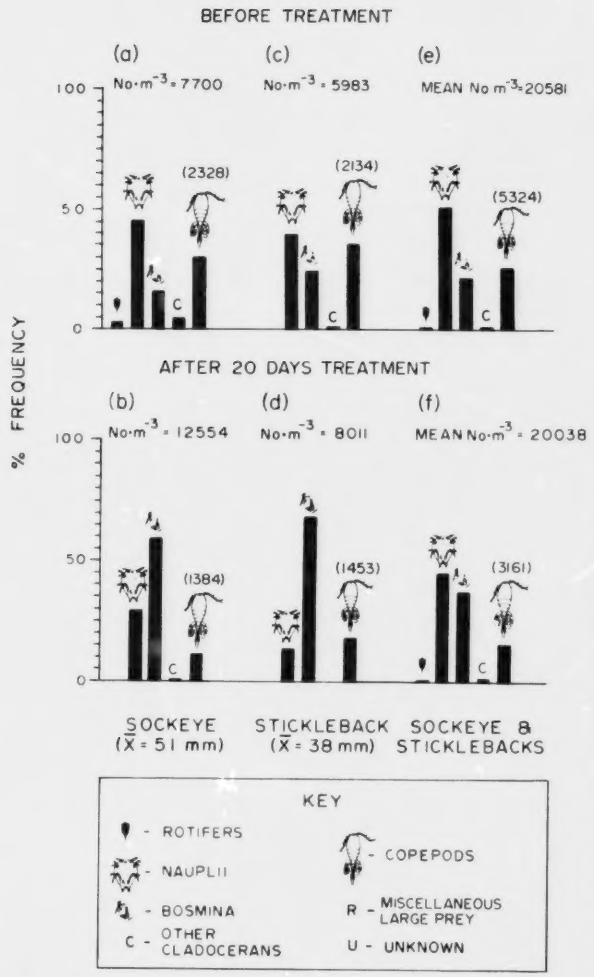

FIG. 9. Frequency distributions (as %) of zooplankton by taxa in enclosures before (a, c, e) and after (b, d, f) treatment with allopatric and sympatric groupings of underyearling sockeye and juvenile sticklebacks. (*Two replicates from sympatric treatments have been pooled.)

At the end of Experiment 2, zooplankton from the fishless control were significantly larger than those from the lake and these were significantly larger than zooplankton from the fish treatment enclosures (Tukey's Procedure — Table 2b). Further, as was the case in Experiment 1, successively higher fish densities in Experiment 2 were associated with zooplankton communities characterized by progressively smaller mean body size, indicating fish predation was responsible for the changes in zooplankton size within the fish-treatment enclosures. Between the beginning and end of Experiment 2, total zooplankton abundance increased 77% in the fishless enclosure whereas it increased only 11% (average) in the fish treatment enclosures (Fig. 8). Thus, fish predation also appears largely responsible for the changes in zooplankton numbers. Total zooplankton abundance remained virtually unchanged in the lake (Fig. 8c, d), which contained a fish density between that in the fish treatment enclosures and the fishless control enclosure.

EXPERIMENT 3. SOCKEYE FRY AND JUVENILE STICKLEBACK (MAY 7–26)

At the start of Experiment 3, small but significant differences existed in sizes of zooplankton among the enclosures and the lake (Fig. 12a, c, e, 13c) (Tukey's Procedure, Table 2c). Fish treatment enclosures contained similar communities of small zooplankters dominated by rotifers, nauplii, and small copepods (Fig 14a, c, e,). The zooplankton composition of the lake sample was similar to that of the enclosures containing fish but had approximately half the total zooplankton density and fewer copepods (Fig. 15c).

In early May, just prior to the start of Experiment 3, four sticklebacks (1 600 fish•ha^{-1}) entered the "fishless" control enclosure through a tear in the wall with the result that the mean size of zooplankton in the fishless enclosure declined dramatically (Fig. 3) to nearly match that of the other enclosures (Fig. 12a, c, e and 13a). However, *B. coregoni*, rather than nauplii and rotifers, was numerically dominant (Fig. 15a). The total abundance of zooplankton in the breached "fishless" control remained dramatically higher than in other enclosures or the lake (Fig. 15), as the level of predation prior to detection and fish removal appeared relatively low.

At the end of Experiment 3, the size distributions of zooplankton within fish treatment enclosures had not changed significantly (K-S, df=2, χ^2 ranges 0–3.13, $P>0.05$ for all comparisons) from those at the start. All enclosures containing fish (mean size of sockeye fry 28 mm, mean size of sticklebacks 33 mm) displayed a decline in overall zooplankton abundance (average 83%) along with a dramatic decrease in rotifer numbers (Fig. 14b, d, f), which resulted in a slight increase in the zooplankton mean size (Fig. 12b, d, f). The number of copepods declined (average 82%) in proportion to the overall zooplankton decrease (Fig. 14b, d, f).

The size frequency distribution of zooplankton from the lake did not change significantly (K-S, df=2, $\chi^2=.0059$, $P<0.001$) between the start and the end of the experiment. The mean size increased slightly from 0.21 mm to 0.27 mm (Fig. 13c, d) and *B. coregoni* dominated numerically (Fig. 15d). Unlike the fish treatments however, samples from the lake showed a large increase in total zooplankton abundance (142%) and an even greater increase in copepod numbers (295%) (Fig. 15).

Ideally, to ensure that differences in numbers or sizes of zooplankton in fish treatment enclosures and the lake were due to differences in fish abundance and not from enclosing the zooplankton community, it is desirable to include comparisons with the fishless control. Unfortunately these data are unavailable as 15 fish (approximately 6 000 sticklebacks•ha^{-1}) invaded the enclosure at some time after initiation of Experiment 3, and compromised the results of the fishless control. Regardless, it appears fish predation had an effect on zooplankton community size as at the end of the experiment sizes of zooplankton sampled from fish treatment enclosures were no longer significantly different from each other (i.e. after 19 days of treatment), and they were significantly smaller than zooplankton from the lake which had a lower density of fish (Tukey's Procedure – Table 2c).

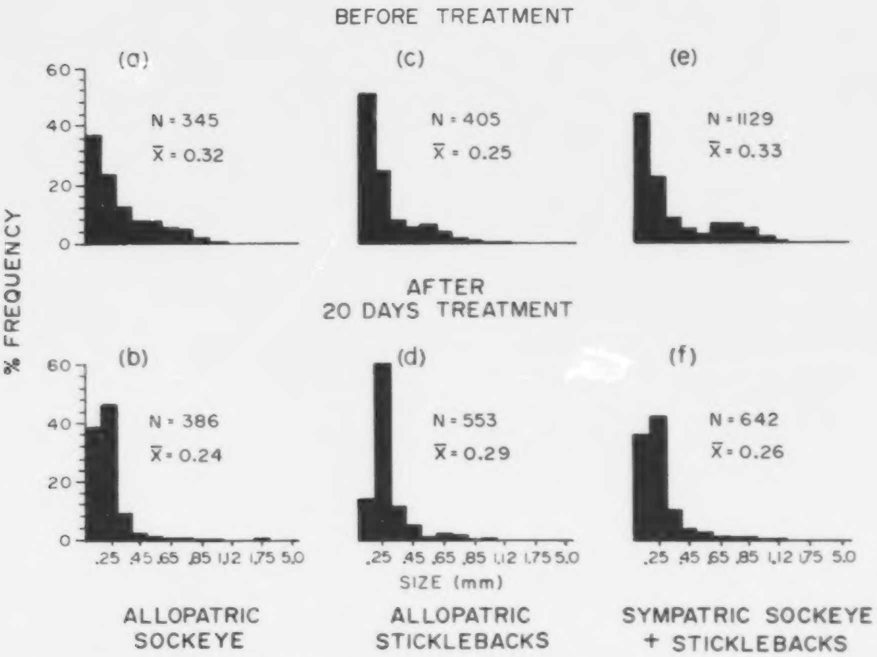

FIG. 10. Frequency distributions (as %) of zooplankton by size in enclosures before (a, c, e) and after (b, d, f) treatment with allopatric and sympatric groupings of underyearling sockeye and juvenile sticklebacks. (*Two replicates from sympatric treatments have been pooled.)

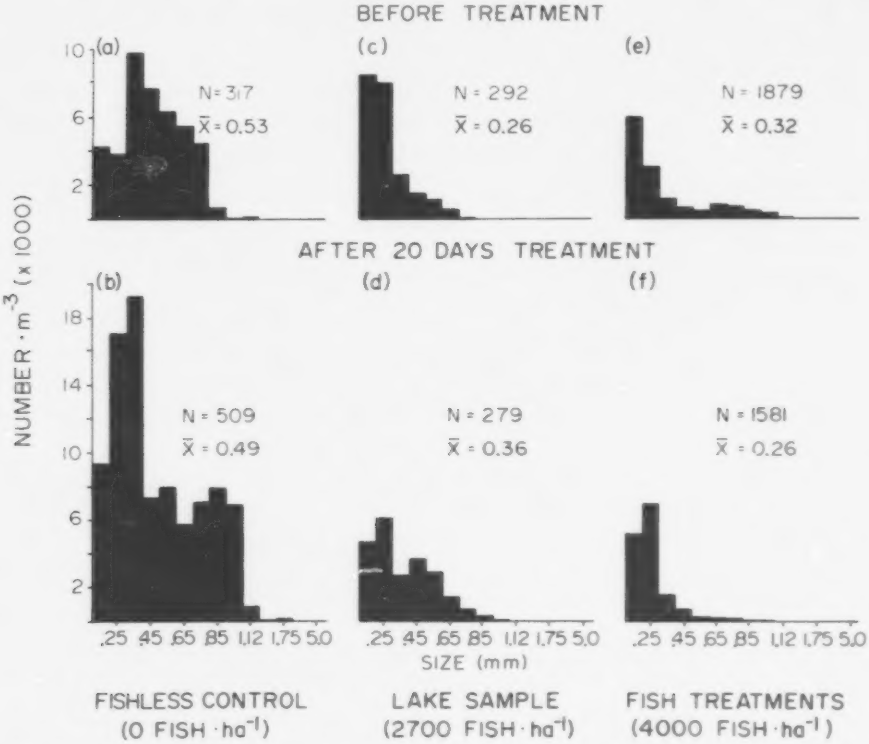

FIG. 11. Comparison of frequency distributions of zooplankton by size sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of underyearling sockeye and juvenile sticklebacks (e, f).

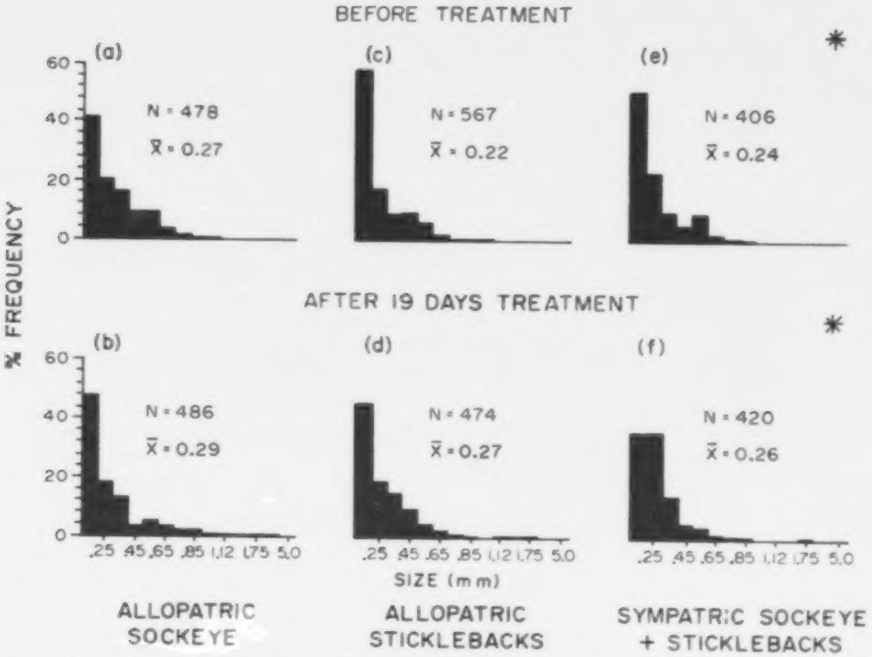

FIG. 12. Frequency distributions (as %) of zooplankton by size in enclosures before (a, c, e) and after (b, d, f) treatment with allopatric and sympatric groupings of sockeye fry and juvenile sticklebacks. (*Replicate sympatric treatments were not pooled as 30 fish invaded enclosure, May 20–26.)

It is unlikely that the major reductions in zooplankton numbers that occurred in fish treatment enclosures (Fig. 14b, d, f) were due to enclosure effects alone as in other experiments major reductions in total zooplankton abundance only occurred when fish were present in the enclosures.

PREY SIZE CONSUMED VS. PREY SIZE AVAILABLE

In all experiments, prey items consumed by fish on the last day of treatment were compared with zooplankton remaining in the enclosures to provide estimates of predator selectivity. Because zooplankton communities were influenced similarly in all fish treatments within each experiment (i.e. all fish treatments at the end of a particular experiment had similar sizes and species of zooplankton), fish diets were pooled across all fish treatments and fish species in each experiment. Fish from Exp. 1 and Exp. 2 ate larger than average sized zooplankton (Fig. 16a, 16b, respectively). Thus, in these experiments, where the zooplankton communities had already shifted to smaller forms over 12 and 20-day periods, respectively, fish fed selectively on the largest prey items available. Size selective predation by fish appears to have been the mechanism by which zooplankton sizes were reduced in enclosures containing fish.

With the exception of a few large prey items, sockeye and stickleback fry in Experiment 3 consumed prey roughly in proportion to their availability (Fig. 16c). The absence of size-selective feeding behaviour by these fish is probably not related to morphological constraints (e.g., mouth gape) because sockeye and stickleback fry in Kennedy Lake are known to consume prey larger than those present in the enclosures (K. D. Hyatt, unpublished data). Accordingly, in Experiment 3, fish predation appears to have reduced the total abundance of zooplankton in test enclosures (compare Fig. 15e, f), without appreciably influencing zooplankton species or size compositions (Fig 12, 14).

Discussion

In three experiments utilizing 3 size categories of sockeye and sticklebacks, zooplankton communities were influenced similarly by sockeye and sticklebacks. In less than 3 wk, the mean size of zooplankton decreased in all fish-treatment enclosures containing sockeye yearlings and adult sticklebacks (Experiment 1) as well as underyearlings of both species (Experiment 2). This size shift was associated with a decrease in absolute numbers of adult copepods (90 and 39%, respectively) and increases in numbers of nauplii and rotifers. Relative to the fishless control, total zooplankton abundance in fish treatment enclosures decreased moderately (average 55%) in the yearling experiment and increased slightly (average 11%) in the underyearling experiment. Zooplankton mean size was not affected by predation by fry of either species (Experiment 3) although total zooplankton abundances were greatly decreased (average 83%). In general, results from all three experiments support the view that both the quantity and quality of zooplankton potentially available as food to sockeye and sticklebacks are subject to rapid reductions under exploitation by either species.

Additional support that fish predation was responsible for the observed changes in zooplankton samples collected from the fish treatment enclosures is evident as similar changes were not observed in the fishless control. In contrast to the fish treatment enclosures, zooplankton samples from the fishless control enclosures in Experiment 1 and 2 exhibited small or no decreases in zooplankton size and copepod abun-

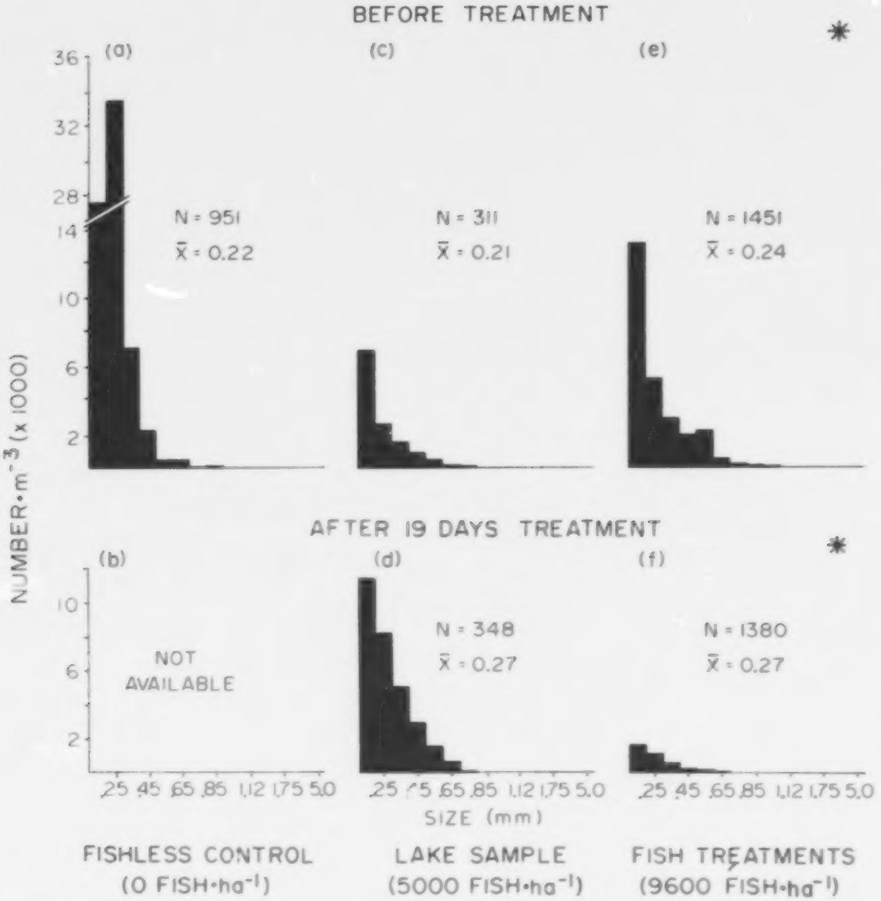

FIG. 13. Comparison of size frequency distributions of zooplankton sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of sockeye fry and juvenile sticklebacks (e, f). (*All fish treatments were pooled except one sympatric replicate which was invaded by 30 fish, May 20–26, were pooled.)

dance, but moderate to large increases in total zooplankton abundance. In Experiment 3 fishless control results were unavailable, but, lower total zooplankton and copepod abundances in the fish treatments (9 600 fish•ha^{-1}) as compared with the lake (5 400 fish•ha^{-1}) suggest that higher fish density in the enclosures had depleted prey disproportionately. The final and perhaps most convincing evidence of the dramatic effect of fish predation on zooplankton size and abundance consists of the results associated with the brief fish invasion of the "fishless" enclosure in early May (Fig. 3). During this time zooplankton abundances dropped from a high of 72 000•m^{-3} to a low of 5 700•m^{-3} and their mean size changed from 0.55 mm to 0.23 mm. Except when invaded, the fishless control contained greater numbers of large-sized zooplankters than the other enclosures, thus confirming the importance of fish predation in influencing the size structure of enclosure zooplankton communities.

In the absence of size-selective predation by fish, size changes of zooplankton in the fishless control appear to occur through a more complicated interaction among differential rates of growth, reproduction, and predation by the various zooplankton species. For example, in Experiments 1 and 2, dramatic increases in the abundance of *Bosmina* (Fig. 5b, 8b) appeared to contribute more to changes in the size of zooplankton in the fishless control than did changes in the abundance or sizes of other taxa. A number of factors favour this outcome. In the absence of fish predation, more of the larger sized zooplankters, made up principally by *B. coregoni* and *D. thomasi*, will survive (Fig. 16) to reproduce. However, the medium sized cladocerans such as *B. coregoni* have a much shorter generation time than the the larger copepods such as *D. thomasi* (Comita 1972; Vijverberg 1980). Consequently, the former species may generally make a greater contribution to increases in zooplankton numbers and changes in zooplankton size when fish are absent for short time intervals lasting only a few days to weeks during the spring and summer.

COMPETITION IN OLIGOTROPHIC LAKES

Three conditions are necessary to demonstrate the occurrence of competition (Pianka 1983) and are outlined below with respect to competition for food between limnetic sticklebacks and juvenile sockeye.

1) Limnetic sockeye and sticklebacks must feed on a common resource that is in short supply. Research by Krogius

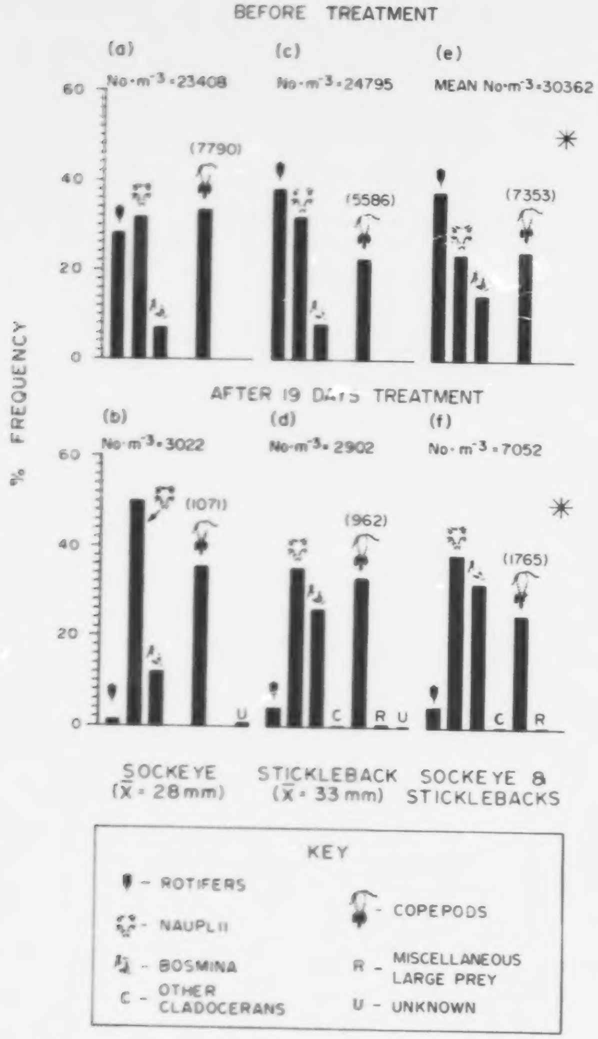

FIG. 14. Frequency distributions (as %) of zooplankton by taxa in enclosures before (a, c, e) and after (b, d, f) treatment with allopatric and sympatric groupings of sockeye fry and juvenile sticklebacks. (*Replicate sympatric treatments were not pooled as 30 fish invaded enclosure, May 20–26.)

and Krokhin (1956b), Greenbank and Nelson (1959), Rogers (1961, 1968), Eggers et al. (1978), and Hyatt (unpubl. data), provides ample evidence that sympatric populations of sockeye and limnetic dwelling sticklebacks feed on similar food resources, particularly on copepods (e.g., *Cyclops* spp.) and cladocerans (e.g., *Bosmina* spp.) as well as emergent insects.

Studies by Brett (1971, 1983) and Hyatt and Stockner (1985) indicate that sockeye growth in typical B.C. sockeye lakes is limited due to an insufficient food supply. Brett (1971) demonstrated that actual weights of juvenile sockeye in Babine Lake were approximately one-half the weights that sockeye were calculated to be capable of achieving under a similar temperature regime but fed a full ration. Brett (1983, p. 5) generalized that "... the freshwater, lacustrine period of the fingerling is one of retarded growth and restricted ration."

2) The amount of food that is available must be determined by consumer use, i.e., sticklebacks must qualitatively or quantitatively affect the food available to sockeye and vice versa. Our results indicate that sticklebacks and sockeye are "trophic analogues" in that sticklebacks can affect the type and amount of food available to sockeye by direct consumption of the resource. The expression "trophic analogues" is not meant to imply that sockeye and sticklebacks have identical feeding habits, given species specific differences in morphology (e.g., mouth shape, gape size and eye diameter) and swimming behaviour. One species may be more efficient than the other, but sockeye and sticklebacks are considered here to function as trophic analogues since they affect each other's food supply within a very short period of time (12–20 days), relative to the amount of time they feed in a growing season (approximately 200 days). The results indicate that these fish are potential competitors.

The influence of these fish on the size and species composition of the zooplankton seems to increase with fish size. Sockeye and sticklebacks larger than fry, affected both the quantity and quality (i.e., size) of zooplankton whereas fry influenced only the quantity. Further, the largest fish used in our experiments (i.e., sockeye yearlings and adult sticklebacks) had a greater effect on the quality of the zooplankton than did fish of intermediate size (i.e., underyearling sockeye and sticklebacks). However, failure of the smallest fish used in our experiments (underyearling sockeye and stickleback fry) to reduce sizes of zooplankton as much as yearling sockeye and adult sticklebacks may have been an artifact of the smaller sizes of zooplankton present at the start of Experiment 3 (i.e., there was very little scope for an overall reduction in size to occur). If these results were not an artifact, this suggests the potential for competition to increase with fish size.

3) The sockeye's fitness must be affected by the resource shortage. If limnetic sticklebacks actually compete with sockeye, then the reduced availability of food must reduce sockeye fitness. In oligotrophic lakes, the weight that sockeye smolts achieve in 1 yr of growth is positively influenced by the amount of zooplankton available per limnetic fish (Hyatt and Stockner 1985). Data from Ricker (1962) and Peterman (1982) suggest that increased marine survival and reduced age at return of adults are correlated with an increase in size at which smolts migrate (usually after 1 yr in freshwater) to the ocean environment. Thus, sockeye fitness seems to be decreased by reductions in lacustrine growth that result from lowered food availability.

All of the conditions necessary to demonstrate competitive interactions between juvenile sockeye and limnetic sticklebacks in oligotrophic lakes have been met. Sockeye and sticklebacks feed on a common zooplankton resource (especially copepods and large cladocerans) which is in short supply. The zooplankton resource available to sockeye is influenced by sympatric populations of sticklebacks, as both species are size-selective predators and consume the largest zooplankters first, leaving the smaller zooplankters. Additionally, sockeye and sticklebacks reduce the abundance of zooplankton. The reduction in the large, energetically most valuable portion of the food supply and reductions in the abundance of zooplankton will probably result in reduced sockeye fitness. Thus, we conclude that sockeye and limnetic sticklebacks compete exploitatively for food.

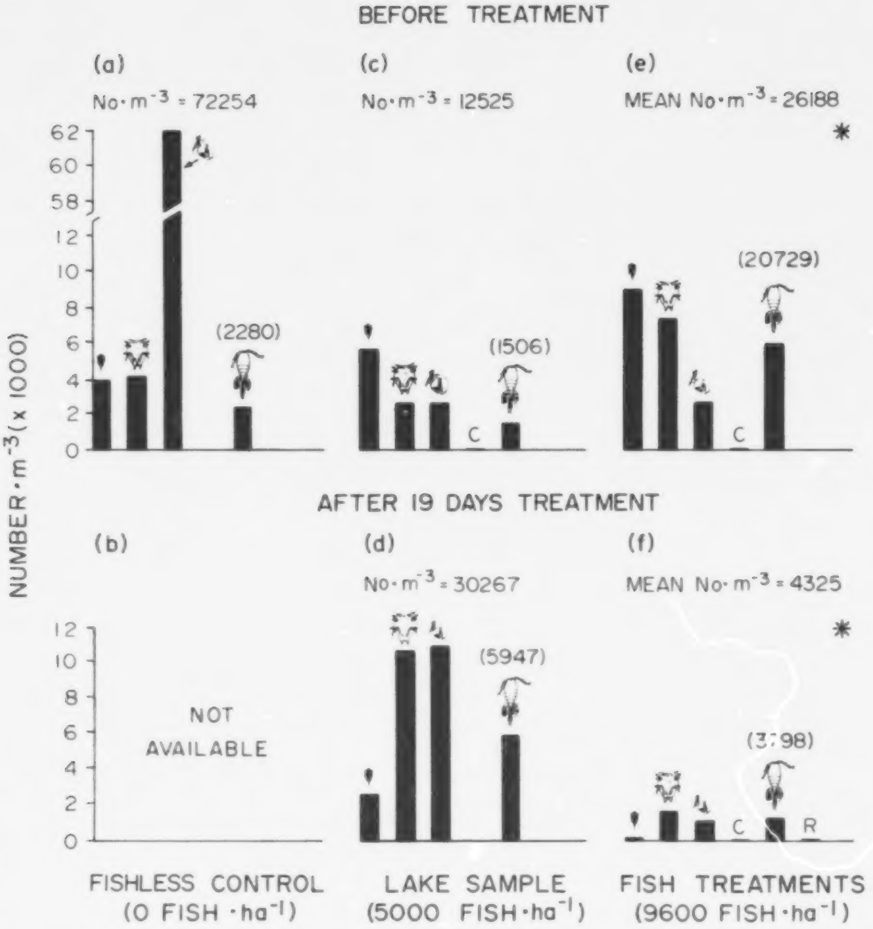

FIG. 15. Comparison of frequency distributions of zooplankton taxa sampled from a fishless enclosure (a, b), Kennedy Lake (c, d), and pooled results from enclosures treated with allopatric and sympatric combinations of sockeye fry and juvenile sticklebacks (e, f). (*All fish treaments were pooled except one replicate of a sympatric treatment; which was invaded by 30 fish, May 20–26.)

STICKLEBACKS AND SOCKEYE PRODUCTIVITY

The findings of this study are relevant to other studies of sockeye production in coastal B.C. lakes. Sockeye productivity is linked to lake productivity, which may vary due to natural, uncontrolled events (e.g., yearly climatic variations; Koenings and Burkett 1987), or due to controlled events such as additions of fertilizers (Stockner and Hyatt 1984). Many stickleback populations have a generation time of approximately one year (Wooton 1976). Consequently, they may exhibit rapid numerical responses to between year changes in lake productivity through both increases in survival of subadults and increased reproductive output of adults. By contrast, sockeye have a 3-yr minimum generation time (Foerster 1968). Thus, numerical responses by sockeye to changes in lake productivity that occur over time periods of less than 3 yr can only be achieved through alterations in freshwater survival of juveniles. This would appear to place sticklebacks at an advantage in responding to short term productivity changes brought about by either natural climatic variability or man-induced events such as lake fertilization. In the present study, we have demonstrated that competition for food between sockeye and sticklebacks in the limnetic zone of lakes has the potential to reduce or eliminate benefits of increased lake productivity to sockeye. In accordance with this we have observed that population responses by threespine sticklebacks have significantly reduced benefits of nutrient additions for sockeye in some years and lakes but not others (Stockner and Hyatt 1984; K. Hyatt, unpub. obser.). The factors that tip the competitive edge in favour of one species or the other are not currently well understood. However, results from the present study indicate that in many B. C. coastal lakes the zooplankton communities of the limnetic zone will be influenced greatly by both juvenile sockeye and sticklebacks and that the production dynamics of these two species are probably interdependent. This suggests that other methods of habitat and fish population manipulation will have to be developed for use in tandem with techniques such as lake fertilization to consistently achieve large increases in sockeye production in such B. C. coastal lakes (Stockner and Hyatt 1984).

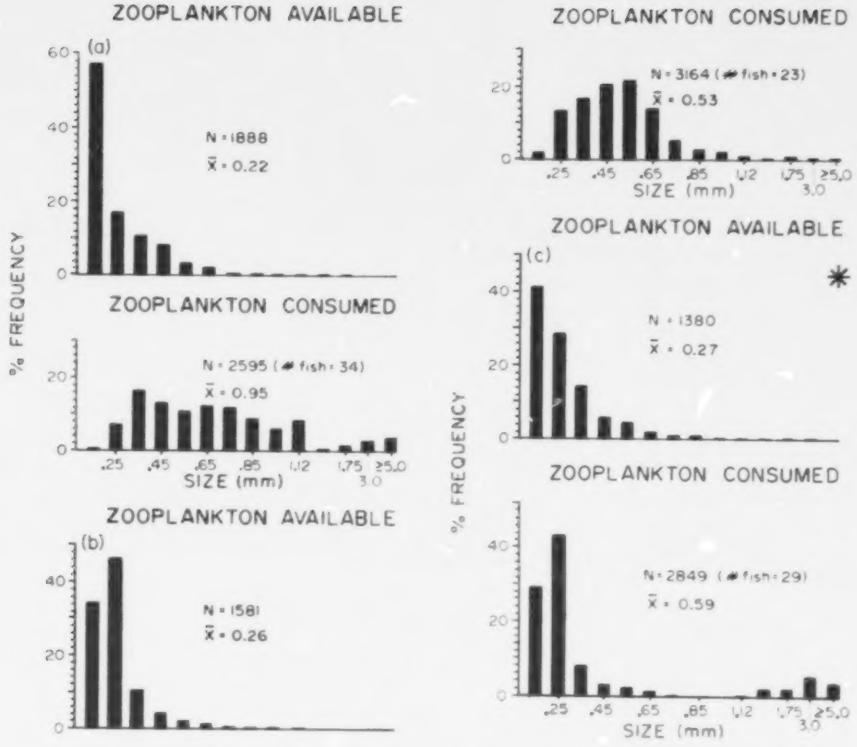

FIG. 16. Size frequency distributions (as %) of prey items consumed vs. prey items available to fish in enclosures at the end of the experiments. (a) sockeye yearlings and adult sticklebacks, Experiment 1 (b) underyearling sockeye and juvenile sticklebacks, Experiment 2, and (c) sockeye fry and juvenile sticklebacks, Experiment 3. (*One replicate from sympatric treatment deleted due to invasion of 30 fish, May 20–26.).

Acknowledgements

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Food Habits of Sockeye Salmon (*Oncorhynchus nerka*) Fry and Threespine Stickleback (*Gasterosteus aculeatus*) in Lake Nunavaugaluk, Alaska, and a Strategy to Improve Sockeye Salmon Survival and Growth

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Abstract

JAENICKE, H. W., M. S. HOFFMAN, AND M. L. DAHLBERG. 1987. Food habits of sockeye salmon (*Oncorhynchus nerka*) fry and threespine stickleback (*Gasterosteus aculeatus*) in Lake Nunavaugaluk, Alaska, and a strategy to improve sockeye salmon survival and growth, p. 161–175. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The diets of sockeye salmon (*Oncorhynchus nerka*) fry (age 0) and threespine stickleback (*Gasterosteus aculeatus*) (ages I and II) were studied in three different littoral habitats of Lake Nunavaugaluk, Alaska, during three 2-wk periods in 1975. The salmon fry fed on zooplankton, particularly *Cyclops scutifer* and copepod nauplii, and diptera (Chironomidae). Age-I threespine stickleback fed mainly on zooplankton, whereas the age-II fish fed mainly on eggs of their own species.

Nonparametric analysis of variance showed diets were significantly different between species and age classes and by time and habitat. Changes in the diets over time generally reflected the seasonal availability of emergent insects, mainly chironomids. Emergent insect trapping revealed that chironomid production was greatest in a sheltered sector of the lake with abundant vegetation and organic enrichment. These protected waters were also the major littoral nursery areas for sockeye salmon in the lake, suggesting survival and growth of sockeye salmon fry from hatcheries could be improved by introducing the fry into calm, chironomid-rich, vegetated shoals. Such shoals provide the fry with nearshore protection against wave-induced turbulence and with vegetation for shelter from predators. Chironomids may offer sockeye salmon fry the bioenergetic advantage of larger prey and an alternate food during zooplankton scarcity.

Résumé

JAENICKE, H. W., M. S. HOFFMAN, AND M. L. DAHLBERG. 1987. Food habits of sockeye salmon (*Oncorhynchus nerka*) fry and threespine stickleback (*Gasterosteus aculeatus*) in Lake Nunavaugaluk, Alaska, and a strategy to improve sockeye salmon survival and growth, p. 161–175. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les régimes alimentaires d'alevins (âge 0) de saumon nerka (*Oncorhynchus nerka*) et d'épinoches à trois épines (*Gasterosteus aculeatus*), d'âge I et II, ont été étudiés dans trois habitats littoraux différents du lac Nunavaugaluk (Alaska) au cours de trois périodes de 2 semaines en 1975. Les alevins de saumon se nourrissaient de zooplancton, surtout de *Cyclops scutifer* et de nauplii de copépodes, et de diptères (Chironomidés). Les épinoches d'âge I se nourrissaient surtout de zooplancton tandis que celles d'âge II se nourrissaient surtout d'oeufs de leur propre espèce.

Une analyse de variance non paramétrique a montré que les régimes différaient de façon significative entre les espèces, les classes d'âge, le moment et l'habitat. Les variations des régimes en fonction du temps reflétaient généralement la disponibilité saisonnière des insectes en émergence, surtout les chironomidés. La capture d'insectes en émergence a montré que la production de chironomidés la plus importante se trouvait dans une zone abritée du lac à végétation abondante et riche en matières organiques. Ces eaux protégées constituaient aussi la principale aire de croissance riveraine pour les saumons nerkas, ce qui porte à croire qu'il serait possible d'améliorer les taux de survie et de croissance des alevins de saumon nerka produits en pisciculture en les plaçant dans des zones à hauts-fonds calmes, riches en chironomidés et à végétation importante. Ces hauts-fonds assurent aux alevins une protection près des rives contre la turbulence induite par les vagues, et la végétation leur offre un abri contre les prédateurs. Les chironomidés peuvent offrir aux alevins de saumon nerka les avantages bioénergétiques de proies plus importantes et leur servir d'aliments de remplacement lorsque le zooplancton devient rare.

Introduction

The decline in abundance of sockeye salmon (*Oncorhynchus nerka*) in southwestern Alaska during the early 1970's (Rowse and Kaill 1983) prompted the Alaska Department of Fish and Game (ADF&G) to consider releasing sockeye salmon fry from hatcheries into underutilized nursery lakes. To evaluate this concept, Lake Nunavaugaluk, a relatively small Bristol Bay lake, was selected for study by the ADF&G and the National Marine Fisheries Service from 1973 through 1977. One aspect of the cooperative research was to select sites around the lake for sockeye salmon fry introductions based on littoral environment, distribution of natural fry, and abundance of emergent Chironomidae, a major prey of the fish (Hoffman 1979).

This paper describes and compares the diets of sockeye salmon fry age 0 (for age determination, see Koo 1962) and threespine stickleback (*Gasterosteus aculeatus*) (ages I and II) in three littoral habitats of Lake Nunavaugaluk during three 2-wk periods in summer 1975. The habitats consisted of an organically rich, vegetated shoal; a barren, wave-swept shoal; and a shoal intermediate in organic richness to the other two shoals. We also describe the association of sockeye salmon fry with emergent chironomid production and vegetation in three physiographically different littoral sectors of the lake, and discuss the survival and growth advantages of fry introduced into calm, chironomid-rich, vegetated shoals.

Study Area

Lake Nunavaugaluk is an oligotrophic lake northwest of Nushagak Bay (Fig. 1). The lake lies 10 m above sea level, is 25 km long, ranges from 2 to 6 km wide, and has a shoreline of 56 km and a surface area of 7 876 ha. Maximum depth is 162 m, mean depth 57 m (Burgner et al. 1969). The water level drops 1 to 2 m from summer to winter, and ice usually covers the lake from November through May. Summer water temperatures reach 14°C near the surface. The lake is clear, with Secchi disk readings of over 16 m; other thermal and chemical characteristics are described by Burgner et al. (1969).

The lake has a single long basin with some shoals in the south sector and even fewer in the north sector (Fig. 1). Virtually no shoals exist along the relatively straight shoreline and steep bottom contour of the middle sector. Rubble and gravel predominate along most of the littoral area, and fine sediments are near Killian, Eagle, and East creeks (Jaenicke et al. 1978). The lake is bounded on the north, east, and west by steep mountains covered with scrubs and small trees, whereas the south end and the outlet, the Snake River, open onto a broad tundra with scattered trees. The combination of frequent, strong winds and low shoreline development (1.64; for equation, see Hutchinson 1957) exposes most of the lake to heavy wave turbulence. However, most shoals in the north sector are protected against heavy wave action

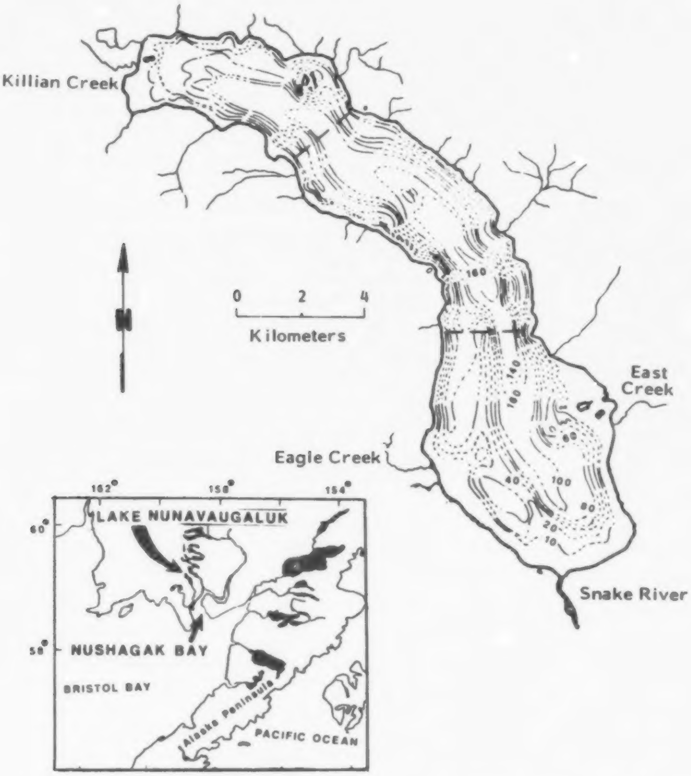

FIG. 1. Lake Nunavaugaluk, Alaska, showing depth contours and sector boundaries.

by the convoluted shoreline and the nearby mountains and hills. In the littoral zone, emergent plants are rare; submerged plants (mostly the algae *Nitella* spp.) are scarce.

Of the 16 species of fish occurring in Lake Nunavaugaluk, the most abundant are threespine stickleback, sockeye salmon, round whitefish (*Prosopium cylindraceum*), and Arctic char (*Salvelinus alpinus*). Sockeye salmon escapements to Lake Nunavaugaluk ranged from 900 to 38 000 fish in 1962–82 (Rowse and Kaill 1983). These escapement numbers are low compared to escapement numbers from many other lake systems in Bristol Bay (Burgner et al. 1969). Sockeye salmon fry sampled in our study were the progeny of 15 300 adults counted through a weir on the Snake River in 1974.

Zooplankton abundance in the lake (Jaenicke et al. 1980) appears to have been adequate for the 1962–82 sockeye salmon production. As an indication of this, Thomason and Jaenicke (1979) found that sockeye salmon smolts from the lake were longer and much heavier than smolts from nearby, mainland river systems.

Methods

Littoral Survey

The littoral area of Lake Nunavaugaluk was surveyed to determine substrate, vegetative cover, depth, and exposure to wave action. During calm days in 6–21 July 1977, a 5 m long skiff was slowly backed at right angles along offshore transects at a series of 232 equidistant stations around the 56 km lake perimeter. To estimate 10 m intervals along each transect, the operator dropped a wood chip in the water by the stern of the boat, then dropped another chip when the bow passed the previous chip. At 10 m intervals, observers viewed and recorded the substrate, vegetative cover, and depth, using an underwater viewing tube and a depth recorder. Appearance from the surface was confirmed by Scuba or snorkeling. Substrate was categorized by the classification of Welch (1952): i.e. sand, gravel, rubble, boulders, and bedrock. Near the mouths of Killian and East creeks, flocculent ooze and other organic material covering the bottom were classified as sand. Vegetative cover was listed as trace (< 10%), light (11–40%), moderate (41–70%), or heavy (>71%). Samples of aquatic plants were taken with a grab at 25 random locations and were identified later in the laboratory. Evidence of exposure to wave action on the substrate was apparent by the wave ripples or lack of organic debris on the bottom. Based on the littoral survey, three habitat types were identified. The length of shoreline included in each habitat category depended upon the similarities in substrate, vegetation cover, depth, and exposure to wave action.

Fish Sampled

Fish were collected with a nylon beach seine along the shore of the lake twice a week during three periods in 1975: (1) 22 June–5 July, (2) 6–19 July, and (3) 20 July–4 August. After 4 August, the sockeye salmon fry and threespine stickleback (ages I and II) moved to deeper waters and were not available to shoreline sampling. The beach seine was 49 m long, 4 m deep in the center, and tapered to 1 m on the ends. Mesh sizes ranged from 3 mm (bar measure) in the bunt section to 19 mm in the wing sections. Sampling locations were selected by a stratified random design based on the three lake sectors (north, middle, and south sectors; Fig. 1) with four random locations fished within each sector each sampling day (Dahlberg 1976). All sectors were usually sampled the same day. By sampling on calm days, we were able to easily deploy the seine anywhere along the shoreline. Immediately after capture, fish samples were preserved in 10% formalin and later processed in the laboratory.

The fish examined for food content were randomly sampled from several hauls which represented different locations and sampling dates within the same habitat and time period. Whenever possible, the fish were sampled proportionately to the total number of fish in each haul.

Size and Age of Fish

The sockeye salmon fry were 23–49 mm fork length. Age-I and age-II threespine stickleback were 26–48 mm and 54–78 mm fork length, respectively. Age-0 and age-III threespine stickleback occurred infrequently and were not included in this study. Age determination of threespine stickleback was based on the fork length of preserved fish. Based on computer analysis of the frequency distribution of the fish lengths (Dahlberg 1978), fish whose length fell within the 95% confidence interval for a particular age group were designated as belonging to that group.

Emergent Insect Trapping

Emergent insects were trapped continuously at the lake between 19–21 June and 24 June–10 September 1975 to determine locations and times of emergence of benthic insects (mainly chironomids or midges) available to the fish. Chironomids were of particular interest because they are a major source of food of young sockeye salmon in early summer in other lakes in Bristol Bay (Merrell 1964; Rogers 1968; Parr 1972) and in Canada (Goodlad et al. 1974). Trapping sites were chosen by dividing the 0–10 m depth contour of the lake into 18 equal areas. Two traps per area were fished over substrate and conditions considered to be representative of the area. Conical, plastic insect traps similar to those described by Sublette and Dendy (1959) were used to sample the insects as they ascended to the surface. Traps were set 0.3 m off the bottom in 3–4 m deep water. Benthic fauna are most abundant at similar depths in mainland Bristol Bay lakes (Rogers 1975). These depths are also frequented by sockeye salmon fry. Catches were counted, measured, and identified every several days during the summer. Lake bottom water temperatures were taken with a thermister thermometer near each trap when it was emptied.

Analysis of Diets

The number of fish necessary to represent the diet of each species and age, in each time period and habitat, was calculated by the method described by Hoffman (1978). It is based on a method for estimating population diversity suggested by Pielou (1966) and assumes that the point where the cumulative diversity of successively pooled stomachs

TABLE 1. Estimated (Est) minimum sample size and actual number (Act) of sockeye salmon (*Oncorhynchus nerka*) and threespine stickleback (*Gasterosteus aculeatus*) sampled to determine their diets, in three time periods (1) 22 June–5 July, (2) 6–19 July, and (3) 20 July–4 August 1975, and three habitats from Lake Nunavaugaluk, Alaska. (na = sufficient sample size not available.)

	Fish sampled (No.)					
	Period 1		Period 2		Period 3	
Fish group	Est	Act	Est	Act	Est	Act
	Killian habitat					
Sockeye salmon, age 0	35	50	50	70	15	40
Threespine stickleback, age I	na	na	40	80	na	na
Threespine stickleback age II	65	75	40	78	80	100
	Outlet habitat					
Sockeye salmon, age 0	50	60	35	40	na	na
Threespine stickleback, age I	na	na	20	33	20	39
Threespine stickleback, age II	na	na	55	74	40	62
	East habitat					
Sockeye salmon, age 0	25	40	30	39	20	30
Threespine stickleback, age I	na	na	30	38	na	na
Threespine stickleback, age II	na	na	35	45	55	70

stabilizes is the point where the cumulative diet can be considered approximately that of the population. The actual number of stomachs examined always exceeds the estimate of minimum sample size (Table 1). In some cases, insufficient fish were available, so the prey of some fish by time and place could not be determined by this method.

Prey in each stomach were counted and identified. Large numbers of prey (>300) were subsampled on a petri dish grid after any uncommon prey items were removed and counted. Organisms were identified with the aid of a stereomicroscope equipped with an eyepiece micrometer. Most zooplankton were identified to genus or species, except for the order Harpacticoida and copepod nauplii. Insects were identified to order, while dipterans (mostly chironomids) were listed by life-history stage. Other prey categories included fish eggs, seeds, and certain broad classifications of invertebrates.

Weight was considered the primary criterion of dietary importance and, in each prey category, was determined by multiplying average dry weight by the number of prey. To obtain an average dry weight, a number of the least digested prey were removed from the stomachs, counted, and dried in a 60°C drying oven, and then weighed on an analytical balance (Hoffman 1979). Because some organisms within a prey category (mainly chironomids) varied considerably in size, weights were separately determined for arbitrarily selected size groups (Hoffman 1979).

STATISTICAL ANALYSIS

A nonparametric multivariate analysis (Mantel and Valand 1970) was used to determine whether diets of fish differed significantly by species, age classes, time, and habitat. This test measures whether "closeness" (i.e. distance) in a set of *p* (prey) variables is related to "closeness" in a set of *q* (fish group) variables, and compares the distance between groups to the distance within groups.

The distance measure used in this test follows a general format which can be specified by the investigator. In this study, the distance measure between two fish (*i* and *j*) was the sum of the absolute differences in their rankings for each prey:

$$Y_{ij} = \sum_{\alpha = 1}^{P} | r_{\alpha i} - r_{\alpha j} |$$

where

P = the number of prey,
$r_{\alpha i}$ = the rank of the i^{th} fish for the α^{th} prey, and
$r_{\alpha j}$ = the rank of the j^{th} fish for the α^{th} prey.

Fish were ranked according to prey percentage by weight in the diet. Group membership (*q* variable) was ranked 1 when individuals *i* and *j* belonged to the same group and 0 when they did not.

The test statistic for judging the relationship between the variables, and a computing procedure for determining its departure from the expected distribution when the null hypothesis is true, are given by Mantel and Valand (1970).

The SPSS two-way analysis of variance program (Nie et al. 1975) was used to determine the numerical relationship of chironomid and sockeye salmon fry catches by sector for late June–early August when the fry occupied the littoral area. One set of factors was tested, i.e. sector of lake and time. For the chironomid analysis, the north, middle, and south sectors had 8, 5, and 23 traps, respectively. Six time periods were used; each time period contained one to five periods of 2 or 3 days. Catches were standardized by dividing the catch per trap by effort. For the fry analysis, 48 beach seine catches were made in each sector in 12 time periods. To stabilize the variance in each cell (chironomid or fry catch), the catches were transformed by Log_{10} (standardized catch + 1). Multiple comparisons of means (Scheffé 1959) were used to determine whether significant differences existed between sectors.

Results and Discussion

DESCRIPTION OF HABITATS AND DIETS

Killian habitat — This habitat, near Killian Creek, is a protected cove typical of the relatively calm littoral habitat throughout the north sector of the lake (Fig. 1). The Killian

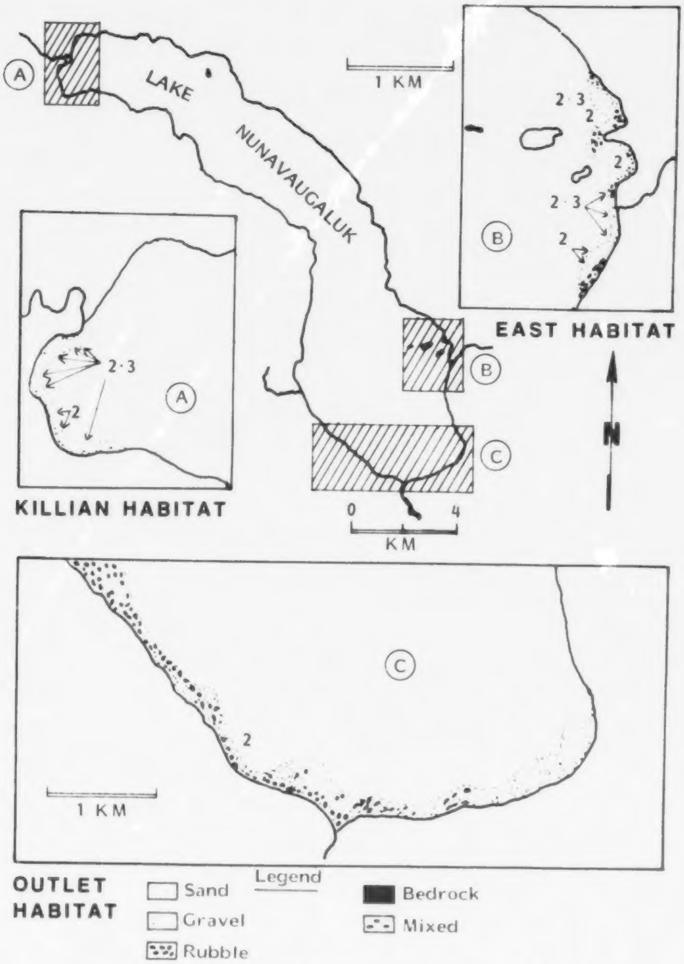

FIG. 2. Substrates and plant cover within the 3 m depth contour of the Killian, East, and outlet habitats, Lake Nunavaugaluk, Alaska. For those respective habitats, the mean distance to the 3 m depth contour was 74, 186, and 231 m. Numbers indicate plant cover: 2 (11–40%), 3 (41–70%).

TABLE 2. Percent composition and classification of substrate and vegetative cover within the 3 m depth contour of Killian, outlet, and East habitats in Lake Nunavaugaluk, Alaska, 6–21 July 1977. (*n* = number of observations made at each habitat.)

Classification	Composition (%) Killian (*n* = 59)	Outlet (*n* = 646)	East (*n* = 216)
Substrate			
Sand	83.1	3.9	66.2
Gravel	16.9	56.2	19.0
Rubble	0.0	39.6	14.8
Boulders	0.0	0.0	0.0
Bedrock	0.0	0.3	0.0
Vegetative cover			
Trace (1–10%)	32.2	16.5	54.6
Light (11–40%)	22.0	0.0	10.7
Moderate (41–70%)	8.5	0.0	3.7
Heavy (71–100%)	0.0	0.0	0.0

habitat extends 1.8 km along the lake shore south of the creek (Fig. 2) and has a substrate composed mostly of sand (Table 2) covered with flocculent ooze and organic detritus, and wood debris from the creek. Submerged vegetation is relatively abundant (Table 2; Fig. 2) and increases steadily with depth.

In this eutrophic habitat, the pelagic copepod *Cyclops scutifer*, copepod nauplii, and chironomids were the major organisms in the diet of sockeye salmon fry (Table 3). During period 1, *C. scutifer* and copepod nauplii constituted half of the diet by weight. Chironomid adults, larvae, and pupae constituted another 39%. By period 2, the numbers of insects had greatly increased. Chironomids, mostly adults, constituted 46% of the diet, and other insects, 12%. The only important zooplankter was *C. scutifer*. During period 3, zooplankton, particularly *C. scutifer* and copepod nauplii, again dominated the diet, while chironomids and other dipterans contributed 33% by weight.

Pelagic zooplankters, particularly the cladoceran *Eubosmina coregoni*, and *Cyclops scutifer*, were the most

TABLE 3. Percentage (by dry weight) of each prey category in the pooled diets of sockeye salmon (*Oncorhynchus nerka*) (age 0) and threespine stickleback (*Gasterosteus aculeatus*) (ages I and II) from the Killian habitat, Lake Nunavaugaluk, Alaska, in periods (1) 22 June–5 July, (2) 6–19 July, and (3) 20 July–4 August 1975. t = trace (<1%).

	Prey in fish diets (%)								
	Age-0 fish			Age-I fish			Age-II fish		
	Period			Period			Period		
Prey type	1	2	3	1	2	3	1	2	3
Pelagic zooplankton									
Cladocera									
Eubosmina coregoni	7	8	3		36		1	8	t
Daphnia longiremus	t	t	t		t		t	t	t
Holopedium gibberum	t	t	t		2		t		2
Copepoda									
Copepod nauplii	18	t	22		2				t
Cyclops scutifer	33	32	42		15		1	3	1
Diaptomus gracilis	2	t			6		2	3	t
Other zooplankton									
Alona sp.	t	t	t		t		t	t	t
Chydoridae			t		t		t	t	t
Chydorus sp.	t				t		t	t	t
Eurycerus sp.							t		t
Harpacticoida	1	2	t		12		t	2	t
Chironomid insects									
Chironomid adults	20	33	9					t	
Chironomid pupae	5	12	4		2		4	2	22
Chironomid larvae	14	1	t		8		11	5	13
Other insects									
Collembola	t	t	t						
Dipteran adult		4	20					t	t
Dipteran pupae								t	
Dipteran larvae					t			t	t
Ephemeroptera									t
Hymenoptera		3						t	
Plecoptera		5						t	t
Trichoptera							t	t	1
Miscellaneous									
Acarina	t	t	t		t		t	t	t
Araneae		t	t					t	
Eggs, stickleback							74	58	56
Gastropoda					14		2	7	t
Nematoda					2		t	t	t
Ostracoda					t		t	t	t
Pelecypoda								t	
Seeds and seedlings							3	11	t

important prey by weight in the diet of age-I threespine stickleback in period 2 (Table 3). The remainder of their diet consisted mostly of benthic organisms such as gastropods, harpacticoid copepods, and chironomid larvae.

Age-II threespine stickleback fed extensively on stickleback eggs which formed nearly three-quarters of their diet by weight in period 1 and over half their diet in periods 2 and 3 (Table 3). The remainder of their diet was quite variable, with immature chironomids being the main prey.

Outlet habitat — This barren, wave-swept habitat is characteristic of the south sector, the largest shoal area in the lake (Fig. 1). The outlet habitat extends 6.8 km along the lake shore and is on both sides of the Snake River (Fig. 1 and 2). Periphyton, organic detritus, and vegetation are scarce along this wide gravel and rubble strewn shoal (Table 2). Such shallow, wave-swept areas characteristically have limited fauna and productivity (Rawson 1930; Welch 1952; Barton and Carter 1982). Wave action is probably the most important factor influencing the composition of the littoral fauna (Moon 1934; Moffett 1943).

The diets of both sockeye salmon fry and age-I threespine stickleback in this habitat consisted mostly of pelagic zooplankton. Sockeye salmon fry fed mainly on *Eubosmina coregoni* and *Cyclops scutifer* in period 1, and *C. scutifer* and copepod nauplii in period 2 (Table 4). Age-I threespine stickleback fed predominantly on copepod nauplii in period 2 and on *Diaptomus gracilis, E. coregoni*, and *Holopedium gibberum* in period 3.

For age-II threespine stickleback, eggs of their own species were again the major prey item and formed almost half their diet in both periods 2 and 3. Other important prey were *Diaptomus gracilis* and chironomid larvae.

TABLE 4. Percentage (by dry weight) of each prey category in the pooled diets of sockeye salmon (*Oncorhynchus nerka*) (age 0) and threespine stickleback (*Gasterosteus aculeatus*) (ages I and II) from the outlet habitat, Lake Nunavaugaluk, Alaska, in periods (1) 22 June–5 July, (2) 6–19 July, and (3) 20 July–4 August 1975. t = trace (<1%).

	Prey in fish diets (%)								
	Age-0 fish			Age-I fish			Age-II fish		
	Period			Period			Period		
Prey type	1	2	3	1	2	3	1	2	3
Pelagic zooplankton									
Cladocera									
Eubosmina coregoni	48	8			6	32		2	7
Daphnia longiremus	10	7			1	1		t	t
Holopedium gibberum	t	t			4	27		t	6
Copepoda									
Copepod nauplii	2	24			65	1		1	t
Cyclops scutifer	28	43			8	t		t	2
Diaptomus gracilis	t	13			5	32		17	17
Other zooplankton									
Acroperus sp.	t	t			t	t		t	t
Alona sp.	t	t			t	t		t	t
Chydoridae	t	t			t	t		t	t
Chydorus sp.	t	t			1	t		t	2
Eurycerus sp.								t	1
Harpacticoida		t			t			t	t
Chironomid insects									
Chironomid adults	6	t				t		t	t
Chironomid pupae	3				4	4		t	9
Chironomid larvae	2	t			6	t		14	8
Other insects									
Collembola		t							
Dipteran adult	t	t							t
Dipteran pupae									t
Hymenoptera		t							
Plecoptera		2						t	
Trichoptera								1	3
Miscellaneous									
Acarina					t			t	t
Araneae								t	
Eggs, threespine stickleback								47	43
Gastropoda								10	
Nematoda								t	t
Ostracoda								3	t
Seeds and seedlings								t	t

TABLE 5. Percentage (by dry weight) of each prey category in the pooled diets of sockeye salmon (*Oncorhynchus nerka*) (age 0) and threespine stickleback (*Gasterosteus aculeatus*) (ages I and II) from the East habitat, Lake Nunavaugaluk, Alaska, in periods (1) 22 June–5 July, (2) 6–19 July, and (3) 20 July–4 August 1975. t = trace (<1%).

	Prey in fish diets (%)								
	Age-0 fish			Age-I fish			Age-II fish		
	Period			Period			Period		
Prey type	1	2	3	1	2	3	1	2	3
Pelagic zooplankton									
Cladocera									
Eubosmina coregoni	1	t	1		7			3	1
Daphnia longiremus	t	7	t		10			9	1
Holopedium gibberum	t	4	t		2			t	t
Copepoda									
Copepod nauplii	62	15	t		19			t	
Cyclops scutifer	6	50	30		5			13	t
Diaptomus gracilis	t	1	t		38			27	9

TABLE 5. (*Continued.*)

	Prey in fish diets (%)								
	Age-0 fish			Age-I fish			Age-II fish		
	Period			Period			Period		
Prey type	1	2	3	1	2	3	1	2	3
Other zooplankton									
Acroperus sp.	1	t	t		t			t	t
Alona sp.	t	t			t			t	t
Chydoridae	t				t			t	t
Chydorus sp.	t	t	t		t			t	t
Eurycerus sp.								1	t
Harpacticoida	8	t	t		t			t	t
Chironomid insects									
Chironomid adults	t	10	31						t
Chironomid pupae	2	3	25		5			4	27
Chironomid larvae	17	2	t		5			15	13
Other insects									
Collembola	t	t	t						
Dipteran adult		1	6						
Dipteran pupae									t
Ephemeroptera									t
Hemiptera									t
Homoptera		1							
Hymenoptera		2	1						
Plecoptera		t	1						
Thysanoptera		t							
Trichoptera					5				t
Miscellaneous									
Acarina	t	t	t					t	t
Araneae			2						
Eggs, threespine stickleback								28	46
Nematoda								t	t
Ostracoda					t				t
Seeds		3	t		3			t	t

East habitat – This habitat (Fig. 1 and 2) is divided by East Creek, is atypical of the south sector, and has conditions between the extremes represented by the other two habitats. East habitat extends 2.8 km along the lake shore and consists of two coves protected by islands in the north and an open shoal in the south. Sand is the dominant substrate (Table 2). Little organic material is present on or in the substrate, except in the northernmost cove where a small stream enters the lake. Scattered vegetative cover is present over much of the habitat, and there are few dense beds of submerged plants (Table 2; Fig. 2). In the protected East and Killian habitats, fine sediments and organic nutrients from nearby creeks accumulate and, thus, allow submerged plants to flourish as they do in other lakes (Macan and Worthington 1951).

Copepod nauplii, *Cyclops scutifer*, and chironomids were the major prey of sockeye salmon fry in this habitat (Table 5). Copepod nauplii predominated in period 1 and *C. scutifer* in period 2. Insects did not increase in the diet until period 3 when the diet was divided among chironomid adults and pupae and *C. scutifer*.

Pelagic zooplankton, particularly *Diaptomus gracilis* and copepod nauplii, comprised most of the diet of age-I threespine stickleback in period 2.

As in the other habitats, threespine stickleback eggs were a major food item of age-II threespine stickleback and formed slightly more than a quarter of their diet in period 2 and almost half in period 3. The remainder of their diet changed from zooplankton, particularly *Diaptomus gracilis* and *Cyclops scutifer*, in period 2 to chironomid pupae and larvae in period 3.

STATISTICAL ANALYSIS OF DIETS

Multivariate analysis showed significant differences ($P \leq 0.001$) between the diets of all fish groups tested (Hoffman 1979). The diets changed between species and age classes and by time and habitat. Table 1 lists the actual number of fish sampled.

DIFFERENCES IN DIETS

Juvenile sockeye salmon and threespine stickleback consume a wide variety of prey. Their diets reflect both temporal (Ricker 1937; Greenbank and Nelson 1959; Merrell 1964; Barraclough and Robinson 1972; McDonald 1973; Manzer 1976) and broad habitat changes (Wallace 1969; Rogers and Newcome 1975). In nearby Lake Aleknagik, Alaska, Rogers (1968) concluded that competition for food between littoral dwelling sockeye salmon fry and threespine stickleback in shoals is probably minimized by the abundance of food and differences in feeding habits.

Similarly, along the shoals of Lake Nunavaugaluk, the diets of both species were different between species and age classes and by time and habitat (Fig. 3, 4, and 5). The sockeye

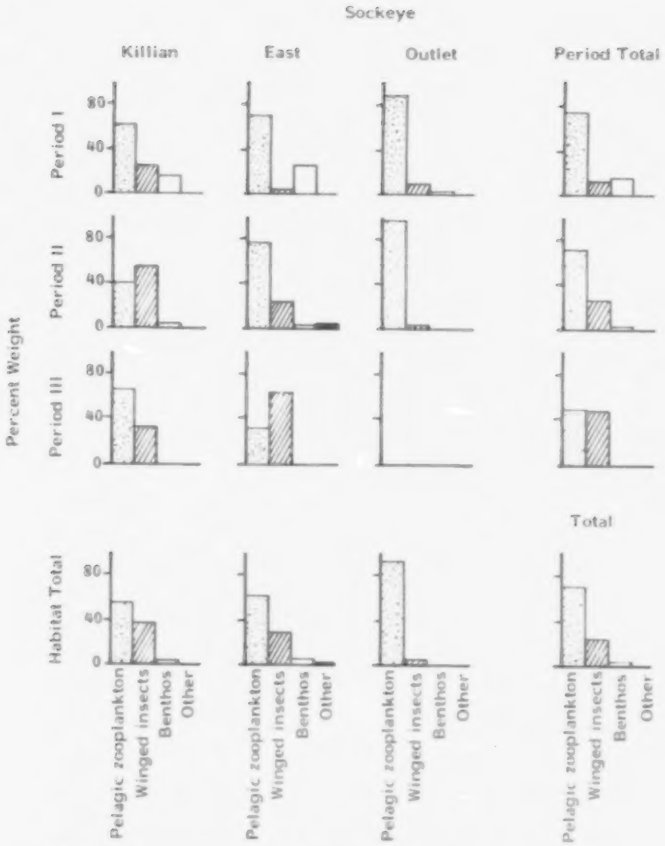

FIG. 3. Percentage composition (by dry weight) for major prey categories in the diet of sockeye salmon (*Oncorhynchus nerka*) fry from Lake Nunavaugaluk, Alaska, in summer 1975. Winged insects include pupae and adults. Benthos includes insect larvae, gastropods, nematodes, ostracods, pelecypods, and non-pelagic zooplankters.

salmon fry fed mainly on *Cyclops scutifer*, copepod nauplii, and chironomids, particularly adults (Tables 3, 4, and 5). Because adult chironomids were an important food of sockeye salmon fry but not of threespine stickleback, the fry apparently fed more near the surface. Chironomids were replaced in the diet of sockeye salmon fry at the outlet habitat by pelagic zooplankton. Less benthos (mainly chironomid larvae) was found in the diet of sockeye salmon than in the diet of threespine stickleback in the same habitat and time period. These observations — sockeye salmon feeding more near the surface and having fewer benthos in their diet than did threespine stickleback — also support the conclusions by Rogers (1968) regarding these species in adjacent Lake Aleknagik.

Age-I threespine stickleback fed more on zooplankton than did sockeye salmon. Chironomids were a minor part (≤10%) of the diet of the age-I stickleback. Gastropods and harpacticoids were important in age-I stickleback diets at the Killian habitat. At the East and outlet habitats, important prey for age-II stickleback were chironomid larvae and pupae and the *Diaptomus gracilis*. At all three habitats, age-II threespine stickleback fed heavily on eggs of their own species.

Previously, stickleback eggs were reported as only a minor prey item in the diets of adult threespine stickleback in sockeye salmon lakes, by Greenbank and Nelson (1959), Rogers (1968), and Manzer (1976). Eggs occur in their diet, presumably, as a result of nest raiding, an activity that is carried out primarily by breeding males (Semler 1971; Kynard 1978; Snyder 1984) and that is probably a response to a shortage of food (Wooten 1971; Snyder 1984). Catch-per-unit-effort (CPUE) of littoral age-I threespine stickleback and sockeye salmon fry increased 200-fold and 31-fold, respectively, from 1974 to 1975 in Lake Nunavaugaluk (Dahlberg and Thomason 1976). This increased abundance of fish, coupled with cold water temperatures after a severe and prolonged winter, could have caused a temporary food shortage that resulted in threespine stickleback eating eggs of their own species.

Generally, benthos decreased in diets as winged insects increased from June to August (Fig. 3, 4, and 5). This decrease probably reflected the maturation of chironomid and other insect larvae. Water temperature is a major factor influencing the emergence of chironomids in northern areas (Hilsenhoff 1966; Danks and Oliver 1972; Welch 1973). The

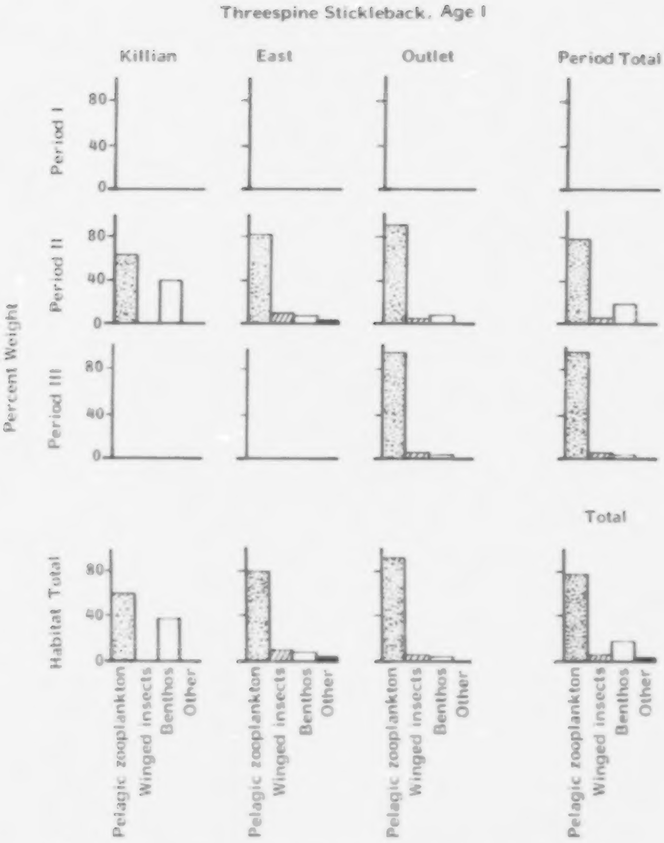

FIG. 4. Percentage composition (by dry weight) for major prey categories in the diet of age-I threespine stickleback (*Gasterosteus aculeatus*) from Lake Nunavaugaluk, Alaska, in summer 1975. Winged insects include pupae and adults. Benthos includes insect larvae, gastropods, nematodes, ostracods, pelecypods, and zooplankton other than the pelagic forms.

number of species of chironomids emerging is directly related to water temperatures in northern lakes (Miller 1941; Morgan and Waddell 1961). In summer 1975, chironomid emergence in Lake Nunavaugaluk was greatest in late July and early August when water temperatures were highest (Fig. 6).

Pelagic zooplankton, the major food of sockeye salmon fry and age-I threespine stickleback, were more abundant in the diets of fish at the outlet habitat than at the Killian habitat (Fig. 3 and 4). Conversely, winged insects, mainly chironomids, were abundant in diets of sockeye salmon fry at the Killian habitat and not at the outlet habitat. The proportions of zooplankton and insects consumed by salmon and age-I stickleback from East habitat were usually intermediate between that measured for the same fish from the Killian and outlet habitats, just as the East habitat was intermediate in biological and physical characteristics between the other two habitats.

Dipterans, mostly chironomids, found in association with vegetation and other organic enrichment, influenced the feeding habits of the fish. In the two habitats (Killian and East) with submerged plants, an average of 36% of the sockeye salmon prey was dipterans (Tables 3 and 5), whereas in the wave-swept, barren outlet habitat, an average of only 6% of the sockeye salmon prey was dipterans (Table 4). These marked variations in the fish diets indicate that emergent chironomids are abundant in some places, scarce in others.

CHIRONOMID ABUNDANCE

In Lake Nunavaugaluk, chironomids constituted 99% by number and weight of the available insect macrofauna, as determined by emergent insect trapping. In late June–early August 1975, about 27 800 chironomids (nearly all were adults or pupae) were caught in 36 traps. Chironomidae are the predominant insect group in lake sediments worldwide (Davies 1976). The chironomid life cycle (egg to adult) can range from many generations per year to one of several years duration (Waters 1979).

The rate of chironomid emergence in the north sector was nearly double that of the south or middle sector of the lake during the period of littoral residence of the sockeye salmon fry. ANOVA and multiple pairwise comparisons of means showed that trap catches of emerging chironomids were significantly higher ($P \leq 0.05$) in the north sector than in the other sectors. Chironomid emergence rates in the south and

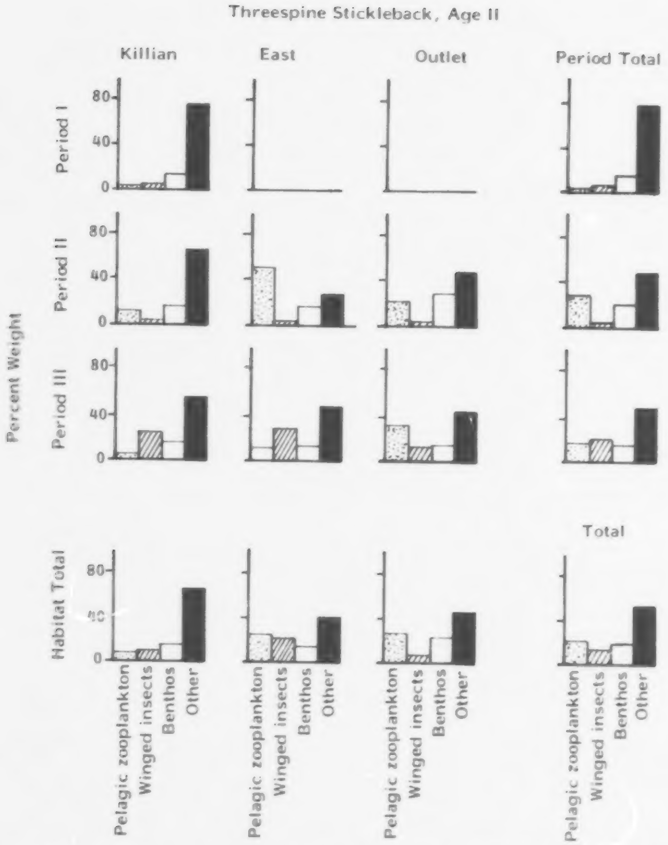

FIG. 5. Percentage composition (by dry weight) for major prey categories in the diet of age-II threespine stickleback (*Gasterosteus aculeatus*) from Lake Nunavaugaluk, Alaska, in summer 1975. Winged insects include pupae and adults. Benthos includes insect larvae, gastropods, nematodes, ostracods, pelecypods, and zooplankton other than the pelagic forms. "Other" consists mainly of threespine stickleback eggs.

middle sectors did not differ significantly. Average midge emergence was 2 396 m^{-2} in the north, 1 280 m^{-2} in the south, and 1 402 m^{-2} in the middle sector of the lake (Fig. 6).

Typically, the abundance of lake benthos, including chironomids, is not evenly distributed (Brinkhurst 1974). Most chironomid larvae are microphagous, feeding on detritus or algae, diatoms, and bacteria (Oliver 1971; Monakov 1972; Moore 1980), and some chironomid larvae also are carnivorous or feed on plant tissue. Moore (1979) reported a positive correlation between the density of chironomid larvae and the amount of organic material in sediments in a Canadian subarctic lake. Chironomid larvae were far more numerous in organic material in well-sheltered bays in the upper littoral zone in Lac la Ronge, Saskatchewan, than in sand or rock in other protected and exposed habitats (Oliver 1960), and were common only near plants in Lake Windermere, England (Humphries 1936). The number of chironomids emerging from plant beds in lakes was greater than from unvegetated habitats (Wohlschlag 1950; Sandberg 1969). Thus, calm, organically rich shoals with macrophytes provide ideal habitat for chironomid production, similar to the Killian and East habitats and to most of the north sector with its many protected coves, organic-covered bottom, and vegetation along the shoals (Fig. 7).

FRY DISTRIBUTION

Most sockeye salmon fry were found in the north sector which is also the location of the major sockeye salmon spawning grounds (Michael L. Nelson, ADF&G, P.O. Box 199, Dillingham, AK 99576, pers. comm.). About one-third of the sockeye salmon spawn in Killian Creek, and the remainder spawn along the shoals throughout the lake (Fig. 7; Michael L. Nelson, pers. comm.). However, relatively few sockeye salmon fry reside along those shoals, except in the north sector. Of the sockeye salmon fry caught in stratified random beach seine hauls in the lake in 1975, 98% were caught along only 28% of the total shoreline. Sockeye salmon fry are often concentrated in relatively small portions of other lakes also (Johnson 1956; Pella 1968; Hartman and Burgner 1972; Goodlad et al. 1974). Two-way ANOVA and multiple pairwise comparisons of means showed that littoral dwelling fry in Lake Nunavaugaluk were significantly ($P<0.001$)

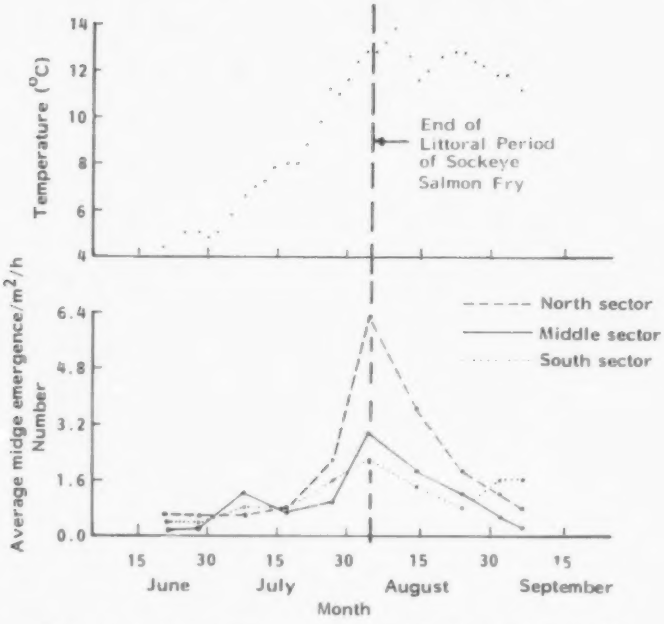

FIG. 6. Average hourly rate (in numbers) of chironomid emergence (per m^2) in the north, middle, and south sectors of Lake Nunavaugaluk, Alaska, 19 June–10 September 1975. Average water temperatures (°C) are indicated.

more abundant in the north sector than elsewhere. The CPUE was 584, 338, and 95 fry per set in the north, middle, and south sectors, respectively. Most fry remained near the calm, chironomid-rich shoals that had submerged vegetation similar to that in the north sector, and avoided habitats without those features (Fig. 7). Similarly, Waters (1969) observed that sockeye salmon fry in nearby Lake Aleknagik preferred littoral habitats with fine bottom materials and some vegetation. Gascon and Leggett (1977) found that the distribution of fishes was strongly influenced by the relative abundance of preferred food sources in Lake Memphremagog, Canada.

ADVANTAGES OF INTRODUCING FRY TO CALM, CHIRONOMID-RICH SHOALS

The similar distributions of naturally produced sockeye salmon fry and chironomids (Fig. 7) in Lake Nunavaugaluk suggest four potential survival or growth advantages which may be realized by introducing sockeye salmon fry from hatcheries into protected, chironomid-rich shoals with vegetation. First, in such areas, the fry are protected against physical harm caused by wave turbulence during the early lake period when fish reside in very shallow water, often only a few meters from shore (McDonald 1969). Heavy wave action along exposed shoals can apparently harm the fry. After violent summer storms, dead fry have been observed along an unprotected beach near lower Talarik Creek, a major sockeye salmon spawning stream in Lake Iliamna, Alaska (Richard B. Russell, ADF&G, P.O. Box 37, King Salmon, AK 99613). Second, the vegetation associated with the chironomid-rich shoals may offer the fry shelter from predators. Predation is usually considered the principal source of mortality of sockeye salmon during their lake residence (Johnson 1965; Hartman and Burgner 1972). Cover, shallowness, and low-light intensity of shoals with vegetation provide effective refuge for sockeye salmon fry and other fishes in Lake Washington (Eggers et al. 1978).

Third, the fry derive a bioenergetic advantage by feeding on larger prey such as chironomids. Fish select their prey on the basis of size, abundance, and ease of capture (Brooks and Dodson 1965). As our study and other studies show (Ricker 1937; Carlson 1974; Goodlad et al. 1974; Eggers 1978), young sockeye salmon often selectively feed on larger prey if available. Based on the average dry weight of the prey of the fish in Lake Nunavaugaluk (Hoffman 1979), the chironomids consumed by the sockeye salmon weighed at least five times that of the zooplankton. As Eggers (1980) noted, by concentrating on the larger prey when available, sockeye salmon reduce the time necessary to meet their energy requirements and, thus, optimize survival or fitness.

Fourth and finally, in chironomid-rich areas, insects provide an alternate food for sockeye salmon fry during littoral zooplankton scarcity, as might result from natural fluctuations in abundance or from cropping down by fish on certain species or sizes of zooplankton. However, because most studies on prey available to juvenile salmon have concentrated only on limnetic zooplankton, research on benthos and littoral zooplankton is needed to further understand the relationship between sockeye salmon fry and their prey.

Based on our observations at Lake Nunavaugaluk, we believe that calm, chironomid-abundant shoals with vegetation are prime areas for introductions of sockeye salmon fry. Because juvenile sockeye salmon suffer greatest mortality during very early residence in lakes (Foerster 1938), further research is needed to clarify both their dependence on the littoral areas of lakes and the carrying capacity of those

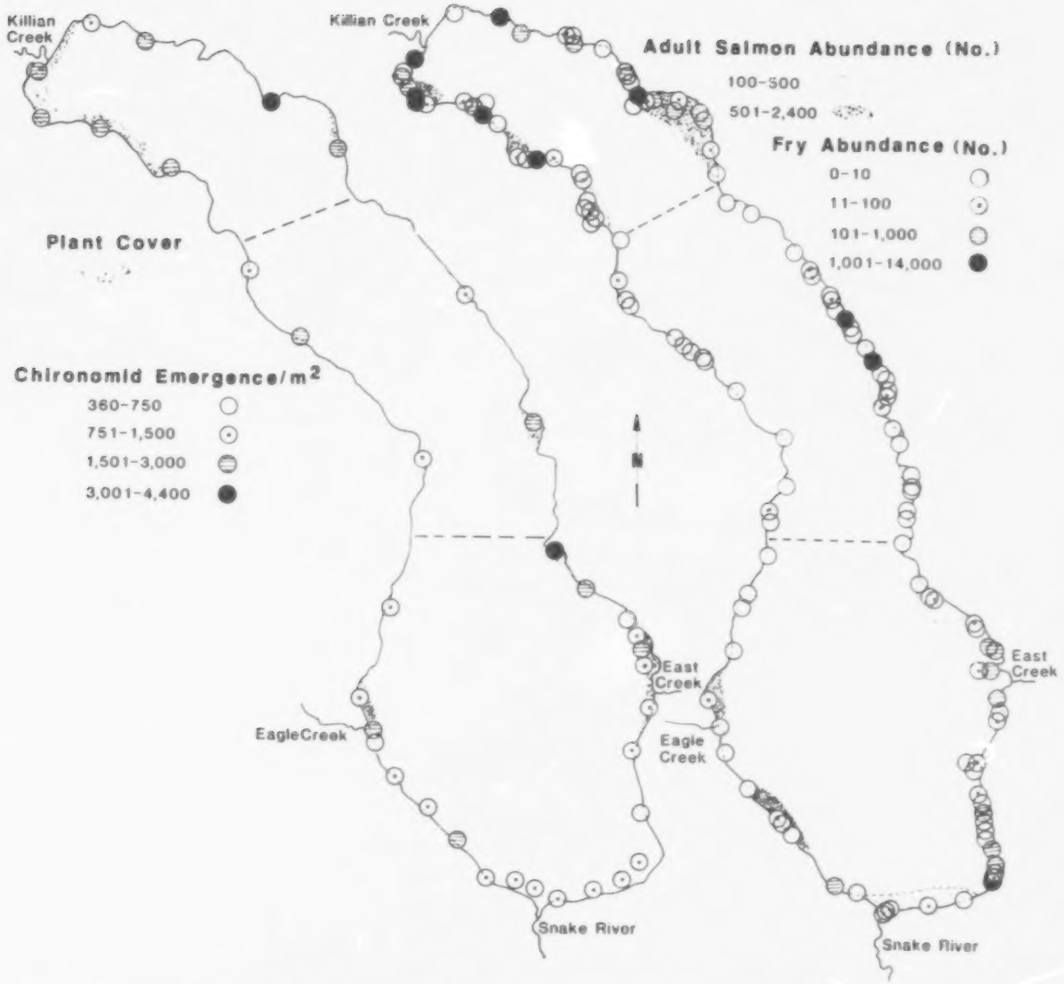
Killian Creek
Killian Creek
Plant Cover
Chironomid Emergence/m^2
360-750 ○
751-1,500 ⊙
1,501-3,000 ⊖
3,001-4,400 ●
Adult Salmon Abundance (No.)
100-500
501-2,400
Fry Abundance (No.)
0-10 ○
11-100 ⊙
101-1,000 ◎
1,001-14,000 ●
N
East Creek
EagleCreek
Snake River
East Creek
Eagle Creek
Snake River

FIG. 7. Chironomid emergence at 36 insect traps around Lake Nunavaugaluk, Alaska, 19 June–10 August 1975, and the distribution of light to moderate beds of submerged vegetation out to 3 m depth in the lake in July 1977. Also indicated is the distribution of beach spawning sockeye salmon (*Oncorhynchus nerka*) in 1974 and distribution of their resulting fry in 1975 in Lake Nunavaugaluk.

areas. Such research may determine whether increased chironomid production along the shoals of lakes is related to the survival and growth of sockeye salmon fry in fresh water.

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Evaluation of Sockeye Salmon (*Oncorhynchus nerka*) Production from the Babine Lake Development Project

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Abstract

West, C. J., and J. C. Mason. 1987. Evaluation of sockeye salmon (*Oncorhynchus nerka*) production from the Babine Lake Development Project, p. 176–190. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The Babine Lake Development Project (BLDP) was initiated in 1962 and consists of three spawning channels on the Fulton River and Pinkut Creek systems, and associated river flow control works. The BLDP is intended to increase the number of sockeye salmon fry (*O. nerka*) rearing in the main basin of Babine Lake and ultimately, to increase the adult returns and commercial catch. A paucity of spawning area had been previously identified as the main factor limiting Babine sockeye production. Mean fecundity of BLDP stocks ranged from 3000 to 3500 eggs per female and was best estimated from body length. Length-independent, inter-annual variation in fecundity was related to the last year of ocean life. Egg retention and other spawning failures increased with female spawner density but did not exceed 3% over a wide range of densities. Egg-to-fry survival averaged 46% in the channels and 21% in the rivers, and was most affected by female spawning density. Efficiency of hydraulic sampling was 63% and the time course of pre-hatch mortality was nearly constant at a daily rate of 0.4–0.6%. Fry production remained efficient at densities as high as one female per 1.25 m^2 of spawning area, the relationship becoming asymptotic at approximately twice that density. The relationship between numbers of main basin smolt and BLDP fry is linear through high levels of production, with fry-to-smolt survival averaging 42.9 percent over 21 years. Adult returns of Fulton and Pinkut origin have increased nearly four-fold since the inception of the BLDP, and are now in excess of 1 M fish annually. Of these, an average of 825 800 are taken in Canadian and U.S. fisheries combined. Commercial landings (741 700/yr) of BLDP sockeye are worth more than $ 6.2 M/yr (1985 Canadian dollars). This amounts to a benefit:cost ratio of 3.02:1, applying a 10% discount rate. History of adult production from the BLDP is compared with abundance trends of non-enhanced stocks of Skeena sockeye.

Résumé

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Le projet de mise en valeur du lac Babine a débuté en 1962. Il est constitué de trois chenaux de frai, situés dans les bassins versants de la rivière Fulton et du ruisseau Pinkut, et des ouvrages connexes de régularisation du débit. Ce projet a pour objectif d'accroître le nombre d'alevins de saumon nerka (*O. nerka*) effectuant leur croissance dans le bassin principal du lac Babine et donc d'accroître les remontées d'adultes et les prises commerciales. On avait déjà déterminé que le manque de frayères constituait le principal facteur limitant la production du saumon nerka dans le lac Babine. La fécondité moyenne des stocks gérés par ce projet variait de 3 000 à 3 500 oeufs par femelle et était le mieux estimée à partir de la longueur corporelle. La variation interannuelle de la fécondité, indépendante de la longueur, était fonction de la dernière année passée en mer. La rétention des oeufs et d'autres facteurs d'échec du frai ont augmenté avec la densité des géniteurs femelles mais n'ont pas excédé 3 %, ceci pour une large gamme de densités. La survie d'oeufs à alevins s'élevait en moyenne à 46 % dans les chenaux et à 21 % dans les cours d'eau. Elle était surtout fonction de la densité des géniteurs femelles. Le rendement de l'échantillonnage hydraulique était de 63 % et le taux quotidien de la mortalité de pré-éclosion était pratiquement constant à 0,4–0,6 %. La production d'alevins est demeurée efficace à des densités aussi élevées qu'une femelle par 1,25 m^2 de superficie de frayère, cette relation devenant asymptotique lorsque la valeur de densité atteignait le double environ. La relation entre le nombre de smolts dans le bassin principal et d'alevins dans l'aire du projet est linéaire même aux niveaux de production élevés, la survie de alevins à smolts, notée au cours de 21 années, étant en moyenne de 42,9 %. Le nombre d'adultes revenant aux cours d'eau Fulton et Pinkut a pratiquement quadruplé depuis la création du projet et s'élève actuellement à plus de 1 million de poissons par an. De ceux-ci, 825 800 en moyenne sont capturés par les pêches canadiennes et américaines. Les débarquements commerciaux (741 700 poissons par an) de saumon nerka du projet ont une valeur qui dépasse les 6,2 millions de dollars par an (dollar canadien de 1985). Ces valeurs représentent un rapport avantages:coûts de 3,02:1 (taux d'actualisation de 10 %). Les auteurs comparent la production de poissons adultes obtenue ces dernières années grâce au projet aux tendances d'abondance des stocks de saumon nerka non mis en valeur de la rivière Skeena.

Introduction

From historic times, most sockeye of the Skeena River system have been produced in the tributary streams of the Babine–Nilkitkwa Lake system (Fig. 1). Fry typically rear in these lakes for 1 yr, then spend 1–3 yr at sea, returning predominantly at ages 3_2, 4_2, and 5_2. The Babine–Nilkitkwa stocks now constitute some 95% of the total production of sockeye in the Skeena River system.

The Fisheries Research Board of Canada began biological surveys on the Skeena sockeye stocks in the mid-1940's, to better elucidate stock and recruitment relations by improving escapement estimates. Spawning grounds of the Skeena sockeye comprise some 100 acres (less than 500 000 m^2). This led Brett (1952) to suggest "the possibilities of a well-planned farming program for fish culture". Johnson (1956; 1958; 1961) believed that the main basin of Babine Lake could support an additional seeding of some 350 M (million) fry. A conservative target of 100 M was set by the Fish Culture Section of the Department of Fisheries and two major tributaries of the main basin: Fulton River and Pinkut Creek (Fig. 1) were selected as development sites to achieve the production target of 100 M fry.

The Babine Lake Development Project (BLDP) associated with this production target presently consists of two spawning channels at Fulton River, one spawning channel at Pinkut Creek, and associated river flow control structures on each system. Channel no. 1 at Fulton River became operational

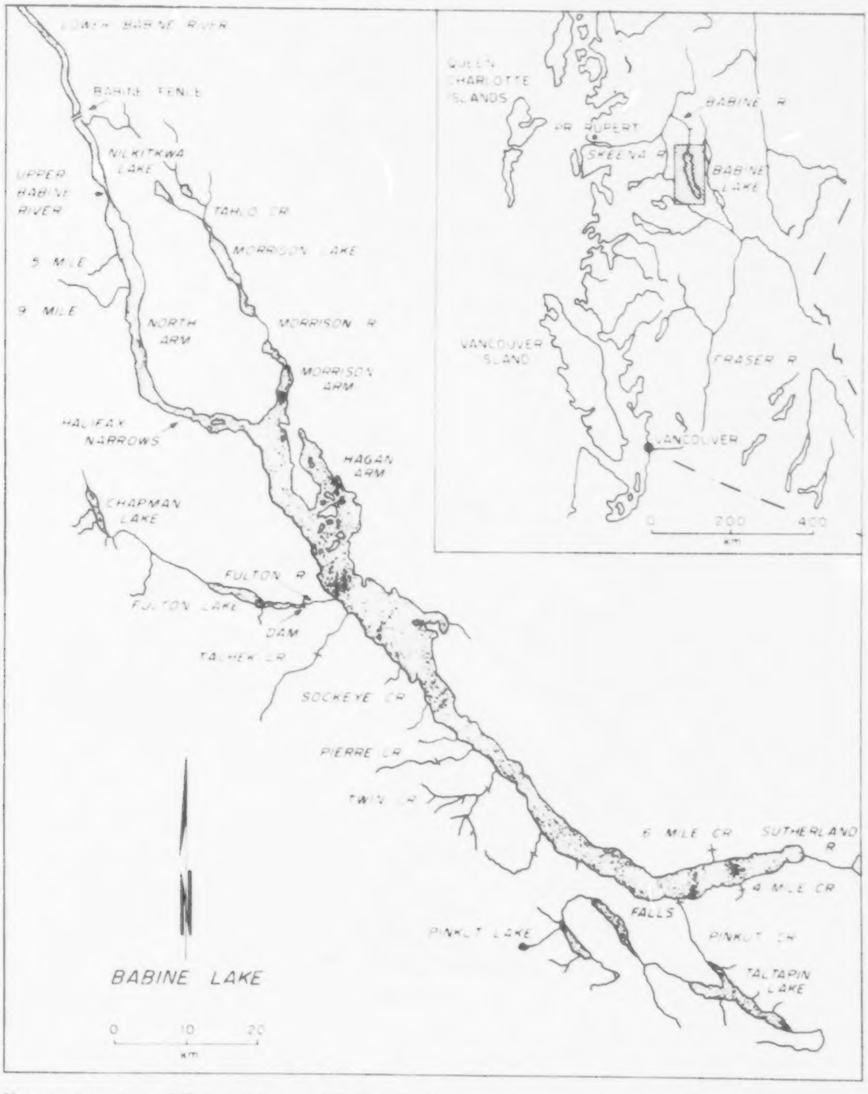
LOWER BABINE RIVER
BABINE FENCE
NILKITKWA LAKE
UPPER BABINE RIVER
TAHLO CR
MORRISON LAKE
5 MILE
9 MILE
NORTH ARM
MORRISON R
MORRISON ARM
HALIFAX NARROWS
HAGAN ARM
CHAPMAN LAKE
FULTON R
FULTON LAKE
DAM
TACHEK CR
SOCKEYE CR
PIERRE CR
TWIN CR
6 MILE CR
SUTHERLAND R
4 MILE CR
FALLS
PINKUT LAKE
PINKUT CR
TALTAPIN LAKE
BABINE LAKE
0
10
20
km
QUEEN CHARLOTTE ISLANDS
PR RUPERT
SKEENA R
BABINE R
BABINE LAKE
VANCOUVER ISLAND
FRASER R
VANCOUVER
0
200
400
km

FIG. 1. Location of Fulton River and Pinkut Creek enhancement projects (BLDP) on Babine Lake, British Columbia.

in 1965, Pinkut channel in 1968, and Fulton Channel no.2 became operational in two stages, in 1969 and in 1971. River flow control structures and permanent adult and fry counting fences were completed in 1968. These facilities and their operations were described by Ginetz (1976) and West (1977). The channels provide 116 500 m^2 of additional spawning area (Table 1) for 186 400 spawners and were expected, with river flow control, to supplement natural production by an additional 100 M fry. Spawning area at Pinkut Creek has been further augmented since 1973 by airlifting surplus spawners by helicopter to an area of approximately 26 700 m^2 of spawning grounds above impassable falls (Table 1). The combined accessible river spawning area is 115 000 m^2, nearly half of the total BLDP spawning area of 231 500 m^2. Sockeye utilize the alluvial fans of both Fulton River and Pinkut Creek when escapement to those systems is unusually high, thus making accurate counts difficult. The extent and outcome of spawning within the lake proper remains incompletely assessed.

TABLE 1. Spawning grounds within the Babine Lake Development Project (BLDP).

Location	Area (1000 m^2)
Fulton River	
Below fence	12.5
Above fence	62.7
Channel no. 1	10.0
Channel no. 2	73.1
Total	158.3
Pinkut Creek	
Pinkut Creek	
Above falls (airlift)	26.7
Fence to falls	10.0
Below fence	3.1
Channel	33.4
Total	73.2
Grand Total	231.5

The BLDP production target was established on the assumption that fry of river and channel origins were equally viable. It was anticipated that the 100 M additional fry would provide some 30 M smolts and 1.25 M adult sockeye, of which 1 M could be harvested in the commercial fisheries. This assumption was tested for the lake-rearing phase by McDonald (1969) and McDonald and Hume (1984) who showed that lacustrine distribution, survival, growth rate and smolt size of channel and river fry were essentially similar, and that the increased fry production has led to substantial increases in the smolt output. Record production of BLDP fry in recent years should allow assessment of the rearing capacity of Babine Lake at unprecedented levels of underyearling population.

In this presentation we examine fry production from the BLDP, some relevant factors affecting that production, and, using a stock reconstruction model, evaluate adult returns of both the BLDP and non-enhanced stocks.

Methods and Materials

Our analyses were grouped according to five consecutive life stages in the rivers: (1) controlling spawner population, (2) estimating egg depositon, (3) monitoring the incubation environment, (4) estimating production of fry, and (5) estimating adult returns.

CONTROL OF SPAWNER POPULATION

A range of operating protocols for seeding the channels and rivers during the past 15–20 yr has provided opportunities to evaluate the effects of variable timing, density, and sex ratio. We control spawner density in the rivers and channels by means of permanent fences, equipped with entry gates and counting stations. Within the channels, spawner entry into specific legs is controlled by adjustable weirs and flow bypass gates. At Pinkut Creek, surplus spawners are airlifted by helicopter to spawning grounds above impassable falls, as previously noted.

ESTIMATING EGG DEPOSITION

For each river system, three females within each centimetre of length are sacrificed at the peak of the run. Their otoliths are taken for age analysis and their eggs are counted individually. We then determine the relationship between number of eggs and female length (post-orbit to hypural plate) at age using regression analysis. Mean lengths of the female populations are then used to calculate mean fecundity, by age class, in each river and spawning channel. We examine fecundity in detail in RESULTS, reflecting nearly two decades of available data.

We estimate egg deposition from the age-specific product of number of females and mean fecundity, corrected for egg retention and complete spawning failure. The latter two statistics are obtained by sampling carcasses throughout the die-off period. The carcasses also provide lengths and otoliths for size and age composition analysis. Sex ratio in the channels is estimated from counts by sex as fish pass through the counting structures, and this ratio is also applied to the adjacent river spawners.

MONITORING THE INCUBATION ENVIRONMENT

Water temperature and volume are monitored continuously. Extensive chemical and physical analyses have been conducted intermittently for both surface and intra-gravel waters. Incubation history is determined by sampling eggs and alevins, using an hydraulic sampler (McNeil 1964) at the eyed stage in late November and again in late January or February at the time of hatching. A standardized hydraulic sampling design has been in place since 1973, and calls for random cross-channel sampling positions at fixed intervals and in representative areas of both rivers and spawning channels. Due to persistent ice cover in Pinkut channel, the January–February sampling was discontinued in 1979. Live and dead eggs and alevins recovered from sampling units of 929 cm^2 (1 ft^2) are recorded. Mean survival rates are calculated from estimates of egg deposition (method given above) and recovery of live eggs and alevins by hydraulic sampling. Confidence limits for mean catches are calculated by fitting catches to negative binomial distributions, using a maximum-likelihood method (Bissell 1972).

ESTIMATING PRODUCTION OF FRY

Prior to 1967, fry migrating downriver were estimated either by the Peterson mark–recapture method, or by a travelling, vertical sampler fished for pre-set time periods at specific locations. In the latter case, the catches were weighted by time, location, and area fished. Nightly migrations were estimated from the relationship over time between net catch, filtration volume, and estimated total river discharge. From 1967 onward, fry have been enumerated at the fences using fixed-position, converging throat traps (Tait and Kirkwood 1962) and, at Fulton channel no. 1, with fan traps (Ginetz 1977). A total migration estimate is obtained by weighting the catches of index traps by time and cross-sectional area fished and summing the resulting nightly estimates over the period of migration. Fry trapping and estimation procedures are described in detail by Ginetz (1977). Egg-to-fry survival is calculated from the estimates of actual deposition and fry production by location.

ESTIMATING ADULT RETURNS

Previous attempts to assess adult returns by means of fin-clipping failed due to high rates of fin regeneration (McDonald 1969). We have estimated adult returns using computerized stock reconstruction techniques. Standardized run timing curves were developed for stocks passing the Babine Fence (Fig. 2). These curves were weighted by their annual escapements and, using the resulting composite curve at the Babine Fence, they were backcalculated to the Tyee Test Fishery (Fig. 2) then the weighted non-Babine stock timing curves were added.

Curves for non-Babine stocks (early and late timed groups) were developed for time of passage past the river fishing boundary, near the Tyee test fishing site. Run timing data were obtained from Aro and McDonald (1968), Smith and Jordan (1973), and Takagi and Smith (1973). More recent data were provided by Kadowaki (CDFO, Nanaimo, B.C. pers. comm.).

We used the curve of timing migration from the Area 4 fishery to the river boundary (Takagi and Smith 1973) to calculate the probable time that each stock spent in fishing Area 4 (Fig. 2). The contribution of each stock to the Area 4 fishery was then calculated from the proportional daily representation of stocks. Their contributions to the Canadian Area 3 X and 3 Y, and to the Alaska (Noyes I. and Cape

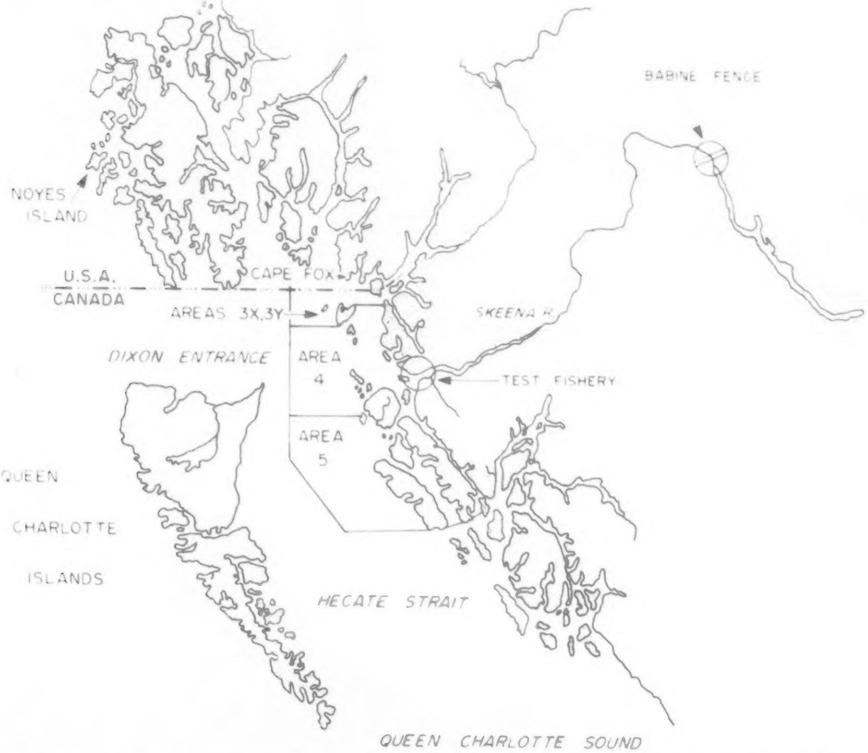

FIG. 2. Locations of the commercial fishing areas, the Skeena River test fishery, and the Babine Fence.

Fox) fisheries (Fig. 2) were estimated by applying the calculated representation of stocks in the Area 4 fishery to estimates of Skeena catch in these other areas. Skeena catch estimates were provided by L. Jantz (CDFO, Prince Rupert, B.C. pers. comm.). Native Food fishery catches of Skeena River sockeye were set in proportion to the escapements.

A Monte Carlo analysis to test the sensitivity of the model to assumptions about stock timing indicated 95% confidence limits of ± 6.5% on estimates of BLDP return. The results are consistent with numbers obtained by accurate counts of the Babine escapement, high resolution of stock timings from intensive tagging studies, and the predominance of Skeena stocks of sockeye in the Area 4 fishery where the principal harvesting of Skeena sockeye takes place.

Results

FECUNDITY

Fecundity of the various Babine stocks typically averages 3 100 eggs per female and is directly proportional to body length (Fig. 3). We used arithmetic values in our analysis following Rounsefell's (1957) finding that differences between the arithmetic and log-transformed values for fecundity of salmonids are of minor consequence.

For Fulton and Pinkut races (Fig. 3, Appendices I and II), comparing the statistically-significant fecundity versus length regressions of 4_2 and 5_2 females, the regression slopes of the 5_2's were generally lower but analysis of covariance

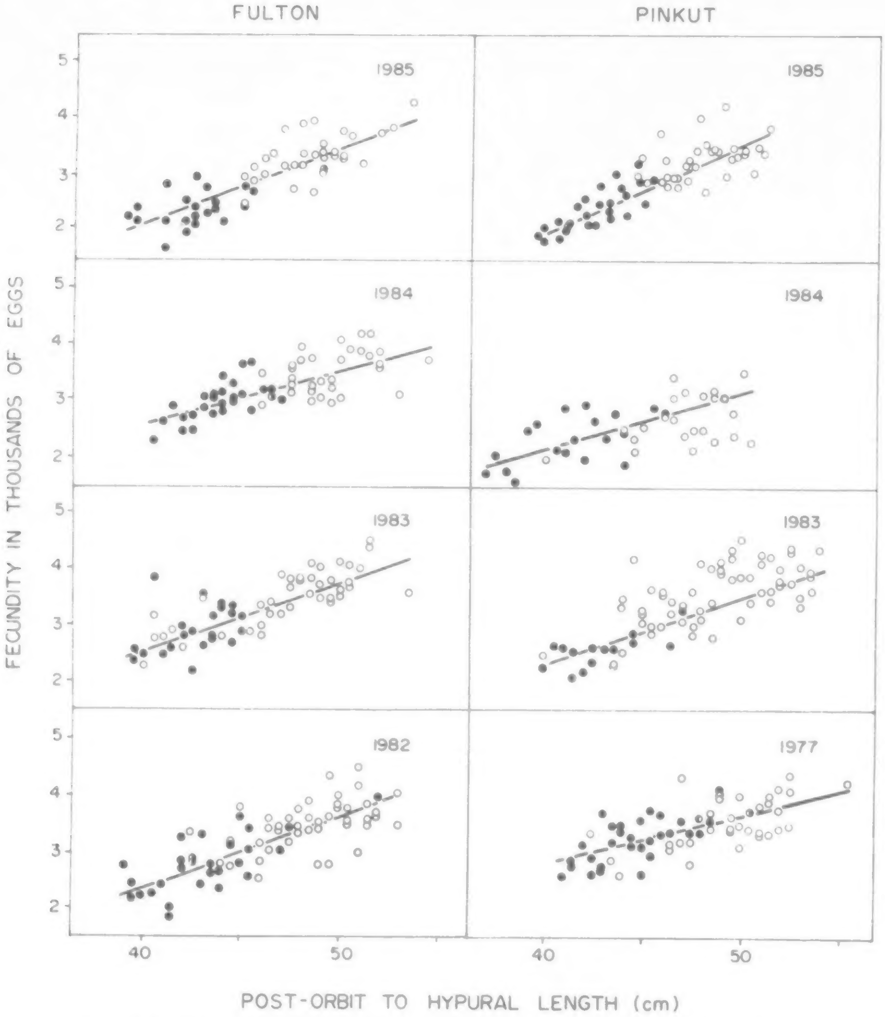

FIG. 3. Linear regressions for fecundity on length; Fulton River and Pinkut Creek sockeye stocks. Symbols as follows: ● — 4_2 females, ○ — 5_2 females.

revealed no statistical differences ($P<0.05$) in slopes or adjusted means in 10 of 11 cases. However, when the 4_2 and 5_2 age data were pooled by stock we did find significant ($P<0.05$) differences between years in adjusted mean fecundity. Annual variation amounted to ± 230 eggs, or 7.4% of the average fecundity. These differences were minor, however, compared to those found among races (non-specific ages) from several river systems as reported by Foerster (1968, p. 125).

Regression coefficients indicated that variation in length accounted for an average of 36% of the variation in fecundity in age-specific regressions, and 48% when age-classes and years were pooled. This variation is similar to the 31-32% reported by Rounsefell (1957) from six years of 4_2 data for the Cultus Lake stock, and the 37% value for Mathisen's four years of 4_2 plus 5_2 data for Pick Creek (Alaska) given by Koo (1968, page 219).

We found no evidence that age *per se* affected fecundity. For sockeye of common length, higher fecundities for younger ocean-age fish have been reported (Rounsefell 1957; Krogius cited in Foerster 1968). Our earlier analysis of covariance showed no dominance of either age class in terms of adjusted mean fecundity and slope. The average difference in adjusted mean fecundity was only three eggs in favor of the 4_2's.

We also tested for possible ocean effects by comparing fecundity-length regressions of 4_2 and 5_2 females from common brood years and from common years of return. While 5_2 females probably share their first 2 years of ocean life with 4_2's of the same brood, they probably share their last year (common year of return) with 4_2's of the subsequent brood. From analysis of covariance, four of nine comparisons by brood year indicated significant differences in slope or adjusted mean values while only one of eleven comparisons by year of return showed a significant difference (all $P<0.05$). This cursory search for possible ocean effects on fecundity suggests that fecundity is more closely associated with the last, rather than the penultimate, year of ocean life. Sea temperature has been negatively correlated with fecundity of pink salmon (*O. gorbuscha*) but freshwater history has not been shown to be of importance in this regard (Rounsefell 1957).

FACTORS AFFECTING EGG DEPOSITION

Magnitude and density of egg deposition are largely the direct outcome of the number of female spawners, their fecundity, and the amount of available spawning area. Deposition has ranged from 76 to 464 M eggs (six-fold) in Fulton River and 10 to 256 M (25-fold) in Pinkut Creek (Tables 2 and 3). The range in numbers of eggs deposited in the channels has been relatively narrow, as follows: Fulton Channel no. 1, 16–58 M (4-fold); Fulton Channel no. 2, 100–220 M (2-fold); Pinkut Channel, 31–100 M (3-fold). These ranges in deposition reflect the operational seeding priority of the channels over the rivers, and the preset targets for density of female spawners in channels. Hence the rivers are prone to greater annual fluctuations in female escapement.

Deposition is secondarily affected by density-dependent changes in female reproductive behaviour and by water

TABLE 2. Egg deposition, fry production, and egg-to-fry survival in Lower Pinkut Creek (fence to falls), Upper Pinkut Creek (airlift area above falls), and spawning channel, 1964–85.

Brood year	Lower Pinkut Creek Eggs (M)	Fry (M)	Surv. (%)	Upper Pinkut Creek Eggs (M)	Fry (M)	Surv. (%)	Pinkut Channel Eggs (M)	Fry (M)	Surv. (%)
1964	255.7	4.5	1.8	—	—	—	—	—	—
1965	53.2	6.9	13.0	—	—	—	—	—	—
1966	24.8	3.7	14.9	—	—	—	—	—	—
1967	40.9	2.7	6.6	—	—	—	—	—	—
1968[a]	19.0	1.9	10.0	—	—	—	30.8	10.4	33.8
1969	10.0	1.8	18.0	—	—	—	37.5	15.2	40.5
1970	16.5	3.3	20.0	—	—	—	37.9	22.0	58.0
1971	13.1	2.2	16.8	—	—	—	30.8	16.7	54.2
1972	21.5	3.0	14.0	—	—	—	96.6	29.0	30.0
1973	30.6	3.1	10.1	25.2	6.0	23.8	97.1	24.1	24.8
1974	30.7	3.0	9.8	49.5	4.6	9.3	93.4	8.3	8.9
1975	20.6	2.6	12.6	52.1	6.6	12.7	67.3	22.3	33.1
1976	35.7	8.1	22.7	48.4	10.9	22.5		under reconstruction	
1977	26.3	6.6	25.1		no airlift		99.5	53.6	53.9
1978	8.3	3.5	42.2		no airlift		50.4	15.1	30.0
1979	42.1	8.7	20.7	46.5	9.5	20.4	92.9	47.5	51.1
1980	31.7	10.8	34.1		no airlift		81.7	42.2	51.7
1981	81.8	20.4	24.9	86.8	21.6	24.9	69.6	57.7	82.9
1982	118.1	28.5	24.1	36.5	8.8	24.1	97.9	68.0	69.5
1983	25.7	7.6	29.6		no airlift		97.7	49.9	51.1
1984	69.6	14.3	20.5	48.4	8.7	17.9	73.2	46.6	63.7
1985	14.9	4.5	30.4	48.8	8.7	17.8	74.4	35.9	48.2
Mean	45.0	6.8	19.2	49.1	9.5	19.3	72.3	33.2	46.2
SD	53.78	6.62	9.62	16.46	4.93	5.41	25.69	18.34	18.15

[a] First year of flow control on Pinkut Creek.

TABLE 3. Egg deposition, fry production, and egg-to-fry survival in Fulton River and the two spawning channels, 1968–85. (M — millions).

	Fulton River			Channel 1			Channel 2		
Brood year	Eggs (M)	Fry (M)	Surv. (%)	Eggs (M)	Fry (M)	Surv. (%)	Eggs (M)	Fry (M)	Surv. (%)
1964	187.0	24.5	13.1	—	—	—	—	—	—
1965[a]	189.0	23.6	12.5	1.2	1.0	82.0	—	—	—
1966	77.5	24.0	31.0	36.9	25.5	69.1	—	—	—
1967	171.6	28.8	16.8	31.9	16.0	50.2	—	—	—
1968[b]	213.6	38.7	18.1	57.7	24.7	42.8	—	—	—
1969	81.7	11.2	13.7	27.8	5.9	21.2	35.0	25.4	72.6
1970	189.9	38.9	20.5	43.3	13.4	30.9	101.7	37.3	36.7
1971	209.3	31.0	14.8	39.4	20.0	50.8	175.2	82.2	46.9
1972	167.4	33.4	20.0	44.6	23.2	52.0	220.4	69.9	31.7
1973	150.0	27.5	18.3	34.3	15.0	43.7	168.7	75.0	44.5
1974	131.5	27.7	21.1	23.6	15.0	63.6	137.6	48.5	35.2
1975	354.2	45.5	12.8	23.6	12.7	53.8	172.4	68.6	39.8
1976	289.3	50.1	17.3	30.3	17.8	58.7	212.8	141.8	66.6
1977	464.3	32.1	6.9	27.4	14.3	52.2	207.1	84.0	40.6
1978	75.9	33.6	44.3	21.7	8.3	38.2	185.6	62.8	33.8
1979	268.3	30.8	11.5	28.3	9.0	31.8	201.4	91.5	45.4
1980	93.9	32.3	34.4	16.3	8.0	49.1	133.3	68.4	51.3
1981	300.8	72.2	24.0	23.7	12.3	51.9	198.1	53.3	26.9
1982	337.4	43.1	12.8	25.6	9.6	37.5	210.6	54.0	26.8
1983	215.0	38.6	18.0	28.9	5.9	20.4	191.8	14.0	7.3
1984	269.7	41.3	15.3	23.7	9.3	39.2	163.2	99.9	61.2
1985	222.8	43.5	19.5	20.3	5.2	25.5	155.3	83.4	53.7
Mean	211.8	35.1	18.9	30.5	13.6	44.1	168.3	68.2	42.4
SD	98.37	12.09	8.39	9.89	6.21	13.51	46.62	29.85	15.99

[a] Eyed egg plant in Channel no. 1.

[b] First year of flow control on Fulton River.

temperature. The amount of egg retention and number of unspawned females was determined by examining adult carcasses following spawning. Regression analysis of the pooled Fulton data (two channels and river) indicated that egg retention and spawning abstention were positively and significantly correlated both with each other and with density of females ($P<0.001$). The relative increases in partially spawned and unspawned females as density increased were both quite low, considering the wide range of spawning densities observed. Both increases averaged less than 3% over all years.

Spawning abstention was also positively correlated ($P<0.001$) with mean water temperature in Fulton River during the first week of September, when the major entry of adults into the river commences. Without exception, all above-average abstentions took place at temperatures exceeding 16°C and reached 20% at 17°C. River temperatures, however, were not correlated significantly with incomplete spawning as reflected in partial retention of egg complement in either Fulton River or its channels. The positive correlation between spawning abstention and river temperature suggests a temperature-induced general stress or blocked behaviour involving commitment to spawning.

FACTORS INFLUENCING EGG-TO-FRY SURVIVAL

Egg-to-fry survival estimates were derived from estimates of eggs deposited and numbers of migrant fry obtained (Tables 2 and 3) as described above. We found only one significant correlation between estimates of survival from hydraulic sampling and estimates of either deposition in the fall, or of fry production (from trapping) in the spring. There was a statistically significant correlation in Channel no. 1 where both arithmetic and geometric mean recoveries of eggs obtained in late November were positively correlated ($P<0.05$) with deposition.

Despite the generally poor correlations, hydraulic sampling provides our only insight into egg mortality in the gravel. The method probably does allow one to detect unusual mortality prior to hatching, and also allows some appreciation of the time course of mortality. From the 12 yr of hydraulic sampling data for Fulton Channel no. 2 (1973–84), the mean survival to late February (25.3%, SD = 8.6) was only 63% of the mean egg-to-fry survival (40.1%, SD = 15.9) derived from estimates of egg deposition and fry production. Hence, sampling efficiency in these channels (63%) was much lower than 90% reported by McNeil (1964). The time course of mortality rate was nearly constant at a daily rate of 0.4–0.6%, using a sampling efficiency of 63% to correct the fall and spring catches from hydraulic sampling, and a conservative fertilization value of 90% based on several works reported in Foerster (1968) for sockeye eggs in natural redds. Recoveries of dead eggs ranged between 20 and 35%, and averaged 24.7% of the estimated deposition. Hence, their sampling efficiency appears to be much higher than for live eggs, approaching or exceeding McNeil's value of 90%. Similarly, more than 95% of the mean mortality (20.4%) over the winter period (90–95 days) was accounted for in the spring sampling.

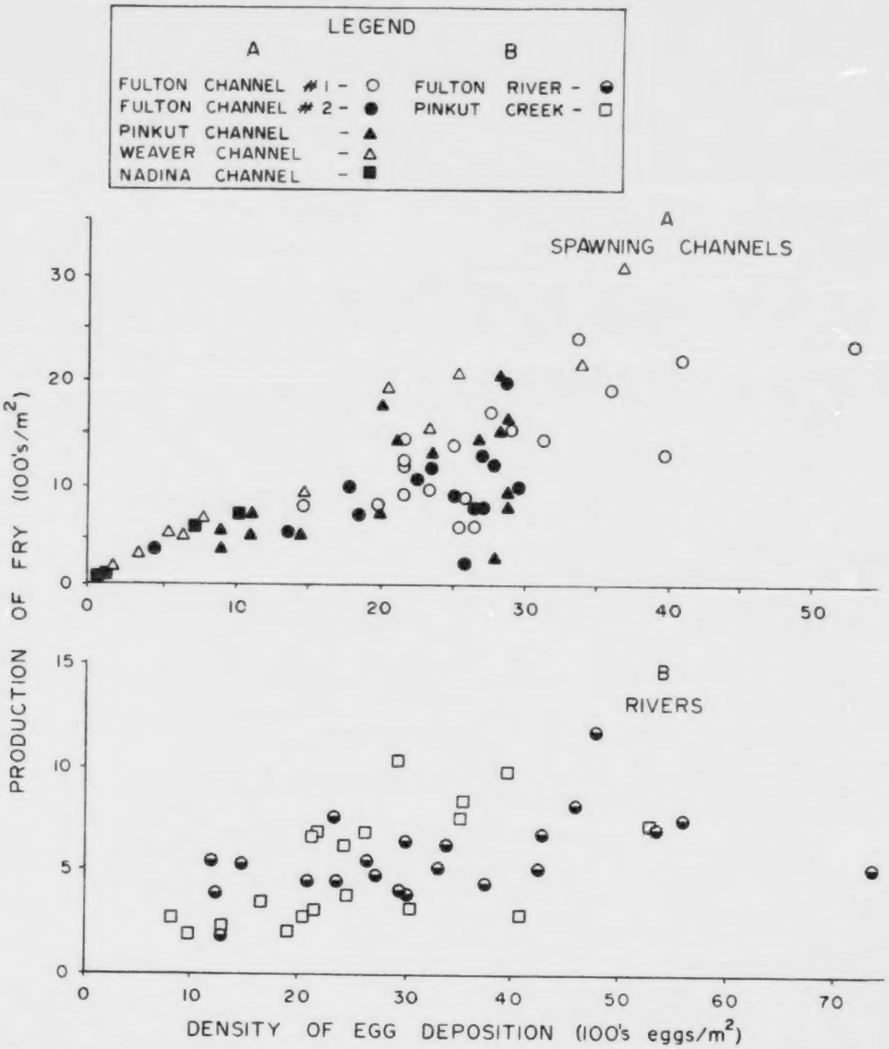

FIG. 4. Production of sockeye fry relative to mean density of eggs at time of deposition in five spawning channels (A) and two rivers (B) in British Columbia. Note differences in scale.

We found significant positive correlations ($P<0.05$–<0.01) between egg density and fry production (Fig. 4.) in both channels and rivers. We advocate general ceilings on egg deposition in the vicinity of 3 000–4 000 eggs/m^2 for both channels and rivers. Within the the BLDP, Fulton Channel no. 1 approached the production ceiling in the first year of operation. A production of 2 350 fry/m^2 was recorded from a density of 3 400 eggs/m^2 and an egg-to-fry survival of 69.1%. We have included fry production data from Nadina River and Weaver Creek (Fraser River stocks) in Fig. 4 by way of comparison. These two sockeye channels were built and operated until 1986 by the International Pacific Salmon Fisheries Commission (Cooper 1977).

Maximum egg-to-fry survival in the several channels has been similar over the usual range (2 000–3 000 eggs/m^2) of egg density (Fig. 5). The wide range in percent surviving at intermediate densities suggests a highly variable but density-dependent mortality mechanism controlling production of fry. The fry production versus egg density plots for channels and rivers have similar form (Fig. 4), but egg-to-fry survival in the two rivers is about halved ($P<0.01$) despite the controlled flow. Fry production in both environments may be approaching maxima at densities greater than 3 000 eggs/m^2, roughly equivalent to a spawning area of 1 m^2/female.

We found no relationship between percent survival and egg density for any of the BLDP channels (Fig. 5A) although significant negative correlations at the 1% and 5% levels were found for Fulton River and Pinkut Creek, respectively (Fig. 5B). Pooling the channel data to expand the range of egg density failed to reduce the ambiguity.

There are at least two major sources of egg mortality: superimposition and siltation. Wave spawning (wherein the spawning beds are used by two or more successive "waves" of spawners) in relation to superimposition was investigated by Ginetz (1972). Pinkut channel was subjected to siltation during the early years of operation. Erosion of the berms through the action of anchor ice and spawning activity, and

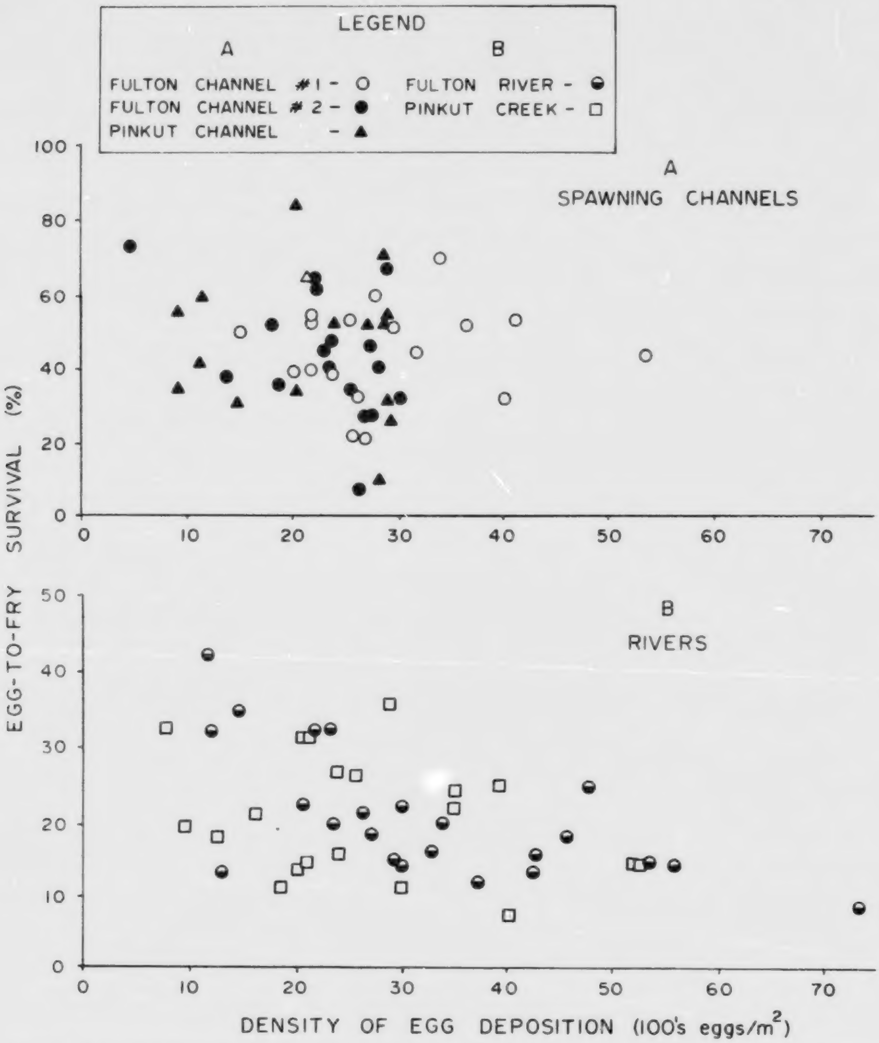

FIG. 5. Relative survival of sockeye fry (%) in relation to mean density of eggs at time of deposition in spawning channels (A) and rivers (B) of the BLDP Project. Note differences in scale.

high sediment loads due to low settling basin capacity, served to reduce survival from a range of 58–25% (mean of 35.4% in 1968–73) to less than 9% in 1974 (Table 2), although mean survival was exceeded in two early years. Following channel reconstruction, the addition of two more settling basins, and intensified annual gravel cleaning, survival of the ensuing 9 brood years (1977–84) has averaged 55.8% and has reached 83% at comparable egg densities. The differences in mean survival and in fry production before and after reconstruction were significant ($P<0.05$).

FRY AND SMOLT PRODUCTION

From the onset of the BLDP, fry production has steadily increased from initial levels of about 40 M to levels commonly exceeding 200 M in the last decade (Fig. 6). Total production of fry has averaged around 190 M (1970–85) of which approximately 130 M (68%) were produced in the channels (Tables 2 and 3). Thus, production in the channels alone is 30% greater than their design target of 100 M fry. Fry production from the two streams, Fulton and Pinkut, (excluding the production from airlifts) has increased since the onset of flow control from an average of 29.6 M to an average of 44.7 M. The spawning grounds above the Pinkut Creek falls have produced an average of 9.9 M fry during the years when surplus escapement justified the airlift. Egg-to-fry survival in upper and lower Pinkut, as indicated by hydraulic sampling, were comparable during those years (Table 3).

Estimated production from both the small Babine streams and from estimated numbers of lake spawners was based on 233 fry/spawner after McDonald and Hume (1984). Fry production (1974–85) from small streams probably declined from that of earlier years, due to reduced escapement. Assumed production from lake spawners rose meanwhile, particularly during the later years of this period, and has averaged about 300 M fry from the last 6 broods (Fig. 6). If, indeed, lake spawners do produce viable fry at such a rate as 233 fry/spawner, their reproductive role could be important. If not, this assumption serves only to underestimate

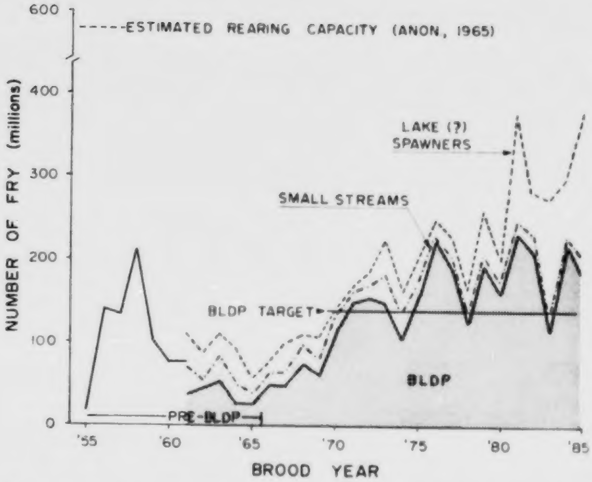

FIG. 6. Numbers of sockeye fry entering the main basin of Babine Lake, British Columbia, 1955–84, and their origins. Estimates of fry for the pre-1961 years are based on August estimates of fry population from Anon. (1965), assuming a 50% survival during the intervening months from emergence.

fry-to-smolt survival in the main lake. The pre-1961 production estimates are based on August population estimates (Anonymous 1965) adjusted upward by applying a generous survival rate of 0.5 between time of lake entry and late summer.

The relationship between fry and smolt production in Fig. 7 is reasonably linear ($r = 0.808$, df = 20, $P<0.001$), suggesting that fry-to-smolt survival is quite uniform (40–45%) for fry inputs exceeding 100 M. The linearity of this regression relationship suggests that there is no compensatory mortality mechanism serving to reduce fry-to-smolt survival even at recent, high levels of fry production.

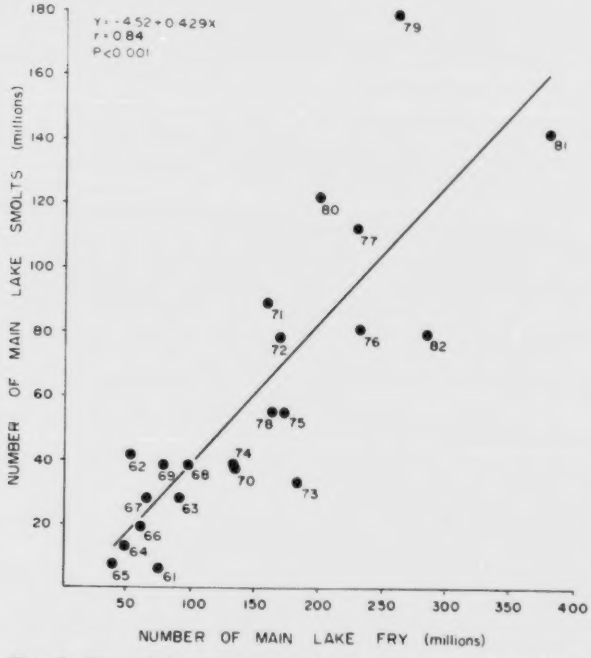

FIG. 7. Size of the sockeye smolt run from the main basin of Babine Lake, British Columbia, 1961–82 brood years, relative to the fry from the BLDP and small streams, excluding potential fry from lake spawners.

ADULT RETURNS, LANDINGS, AND ESCAPEMENTS

Total returns, landings, and escapements of Skeena sockeye derived from the stock reconstruction model have been averaged over two time periods: 1958–1971 (pre-BLDP) and 1973–85 (BLDP), see Table 4. Data for 1972 were omitted to equalize the number of years in the two time periods and to recognize that 1973 marks the 4-yr-old return of brood year 1969 whose fry production reached the halfway point in the BLDP target of 100 M additional fry.

Total Skeena sockeye returns have increased by 87%, from 1 322 241 in the first time period to 2 476 361 fish in the second period, and total landings (Canada and USA) have more than doubled, from 633 685 to 1 357 837. Overall (1958–85), annual total returns and landings of Babine stocks have both doubled but returns to Babine River and the small tributary streams have decreased by 22 and 28%, respectively. Of the non-Babine stocks, returns of the "late timing" group have not declined but the "early" group has declined significantly (56%), at least partly because of intense exploitation during 1973–76 (Fig. 8). The non-Babine stocks underwent extensive decline in the 1950's, almost two decades prior to the first, increasing returns to the BLDP. Since that time, the early stock grouping showed an evident decline during the late 1960's to late 1970's from >30 000 to <10 000, then recovered to moderate escapement levels (~20 000) thereafter, accompanied by marked reductions in harvest rate.

The estimated landings of BLDP sockeye from the various fisheries are given in Table 5. Some 68% of these landings (both time periods) were taken in Area 4 (40–41% of the return), the remaining landings (5–7% in each) were from the Alaska, Areas 3 X and 3 Y, and Native Food fisheries. Since the BLDP, the average return of Fulton plus Pinkut sockeye has increased nearly four-fold, from 358 000 to 1 359 000. More than 1 M fish have been added to the average annual pre-BLDP runs. The Native Food fishery has shown the lowest rate of increase, and the fishery in 3 X and 3 Y has shown the highest.

Discussion

Fry production has exceeded the design target of each BLDP facility illustrating that large spawning channels can be effective producers of sockeye fry. Some factors which may determine fry production have been identified but the associated processes and their interactions that dictate production levels require clarification if we are to maximize production without sacrificing quality. For example, fry production approaches a maximum of 1000 fry/m^2 in the rivers and 2 500 fry/m^2 in the channels when deposition is about 3 000 eggs/m^2 or more (Fig. 4). This corresponds to a density of 1 female/m^2.

At routine egg densities of 2 000–3 000 eggs/m^2, egg-to-fry survival has averaged 46.3% in the channels compared to 20.8% in the rivers. This significant difference ($P<0.01$) reflects the combined benefits of selected gravel size, control of water flow and spawner density, and reduced silta-

TABLE 4. Estimated average returns, landings (U.S. plus Canadian commercial plus Native food), and spawning escapements of Skeena River sockeye stock groupings during 1958–71 (pre-BLDP) and 1973–85 (BLDP), from the Skeena stock reconstruction model.

Stock grouping	1958–71	1973–85	Magnitude of change
Fulton/Pinkut (BLDP)			
Returns	358 410	1 359 558	3.79
Landings	212 441	825 729	3.89
Escapements	145 969	533 829	3.66
Babine River			
Returns	562 388	410 949	−0.27
Landings	303 846	242 845	−0.20
Escapements	258 542	168 104	−0.35
Babine Lake			
Returns	284 789	529 411	1.86
Landings	144 797	334 089	2.31
Escapements	116 267	195 322	1.40
Babine streams			
Returns	141 440	94 285	−0.33
Landings	60 319	36 361	−0.40
Escapements	81 121	57 924	−0.29
Babine Totals			
Returns	1 347 027	2 394 203	1.78
Landings	721 403	1 439 024	1.99
Escapements	625 624	955 179	1.53
Early non-Babine streams			
Returns	55 377	21 145	−0.62
Landings	27 165	7 236	−0.73
Escapements	28 212	13 909	−0.51
Late non-Babine streams			
Returns	41 658	37 565	−0.10
Landings	21 936	23 265	1.16
Escapements	19 722	14 300	−0.28
None-Babine Totals			
Returns	97 035	58 710	−0.40
Landings	49 101	30 501	−0.38
Escapements	47 934	28 209	−0.41
Skeena R. Totals			
Returns	1 444 062	2 452 914	1.70
Landings	770 504	1 469 526	1.91
Escapements	673 558	983 388	1.46

tion. The two to three-fold range in channel survival, however, is equivalent to that for the rivers at similar egg densities, and do not stem from errors in estimating fecundity, egg deposition, or fry production which do not exceed 10%. Hence, we suggest that positive and negative factors common to both environments: biological factors such as spawner interaction, redd superimposition, sex ratio and proportion of jack sockeye, reproductive state of spawners, gamete viability or disease; and physical factors such as temperature (effects on spawner activity, on fertilization and embryo development etc.), and scouring of the gravel bed by anchor ice may have quantitatively similar impacts on survival in both channels and rivers.

Egg-to-fry survival in the spawning channels is about half that routinely found in alternate hatchery technologies so we have considerable incentive to quantify the biological factors identified above, and to determine their potential interactions and effects as they may affect fry production. Operationally, successive wave spawning that leads to redd superimposition is minimized by loading the channel sections one at a time, and preventing upstream movement of later arriving fish into fully loaded sections.

A fishery for jacks at the Babine Fence exerts some influence on the proportion of jack sockeye in the BLDP escapements but does not otherwise affect the sex ratios of the component stocks. Sex ratio could also be controlled at section fences within the BLDP but we have insufficient manpower to assess the effects of such manipulation on egg-to-fry survival and fry production at present. We aim to stabilize density of female spawners at 1/1.25 m^2 for five years and to increase experimentation in production operations. Extensive manipulation of spawning population in the BLDP could only be justified if it leads to an improved understanding of the underlying causes of variability in survival to the migrant fry stage.

LAKE REARING CAPACITY AND SMOLT YIELD

Fry densities observed in the North Arm of Babine Lake and in Nilkitkwa Lake (Fig. 1), led Johnson (1958) to conclude that to achieve comparable densities in the main basin would require an input of some 600 M fry, ostensibly without exceeding the rearing capacity. Thus, the current combined production of 250–300 M fry from the BLDP and wild

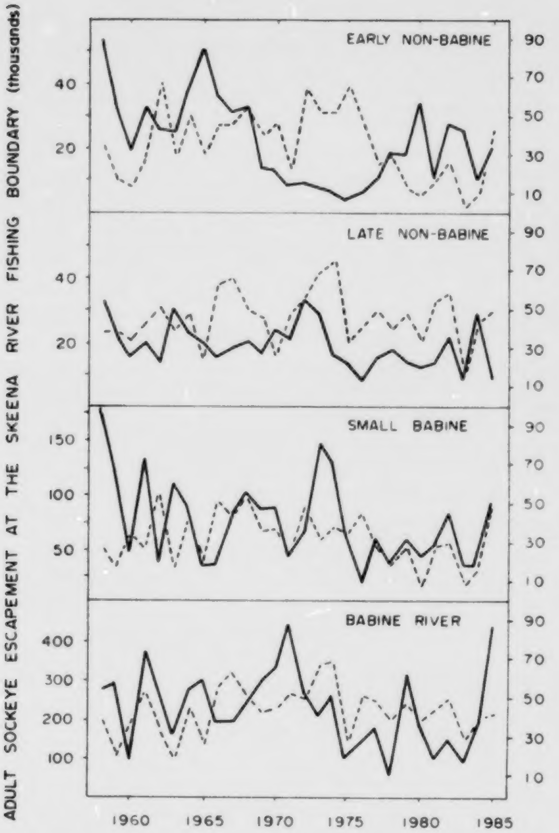

FIG. 8. Annual harvest rates in Area 4 (dashed lines) for the non-enhanced stocks of Skeena sockeye, and their escapements past the Skeena River Fishing Boundary (solid lines), 1958–85.

Babine stocks (300 M includes the potential production from lake spawners) would be expected to utilize about half of Johnson's estimated rearing capacity in the main basin.

The persistent linear relationship between fry and smolt production in the main basin suggests that rearing capacity has not been exceeded. Declining mean size of smolts since BY1969 (Macdonald et al. 1987) could be interpreted as evidence that the rising production of fry and smolts is challenging food resources. These authors have shown a clear link, within cohorts, between smolt length and subsequent survival to return, and smolt size is known to affect marine survival of other salmonids. However, mortality assumptions associated with smolt size relations within cohorts should be applied with caution to size relations between cohorts. Intense gradients of size-selective mortality within a juvenile population may cause only small differences in mortality rates among populations differing slightly in mean size (West and Larkin 1987). Thus, mortality attributable to annual variations in mean size of Babine smolts may be of minor consequence, considering that the range in mean annual length of Babine smolts during the past 25 years only amounts to some 10% of the smallest mean length. In contrast, range in mean annual length exceeds 35% in smolts from Chilko Lake (Fraser River system) where size is not correlated with 25 years of adult return (I. Williams, CDFO, Cultus Lake, B.C. pers. comm.).

Whether or not the length and weight trends in Babine smolts persist or will affect adult return remains conjectural. Smolt biomass is increasing in Babine Lake and it may be profitable to accept reduced survivals, in favour of increased overall returns. The processes producing the more than four-fold range in smolt biomass from similar, high numbers of fry should command our attention since mean smolt size and size of smolt population are not correlated.

HARVEST AND CONSERVATION PROBLEMS

Traditional mixed-stock fishery problems are well documented on the Skeena. Larkin and McDonald (1968) suggest that the non-Babine stocks are inherently less productive than are the Babine stocks and warrant lower harvest rates. Following the Babine Slide in 1951 and a consequent shift of harvest pressure, the non-Babine stocks underwent an extensive decline in the mid-1950's. Failure of these stocks to rebuild (prior to the first BLDP returns in the early 1970's) was noted by Ricker and Smith (1975) who speculated that lake productivity could have declined due to reduced fertilization from the carcasses of diminished escapements. The largest single stock reduction (> 100 000 fish) among non-enhanced, Skeena sockeye has occurred in the Babine River stock (Table 4). This decline may be partially due to circumstances unrelated to the BLDP since the latter half of the Babine River run occurs coincidentally with the Babine River pink salmon run. Babine pinks have increased from a few thousand fish in the early 1950's to several hundred thousand in recent years and are now subject to an expanding commercial fishery. This fishery is creating an interception problem for the Babine River sockeye.

TABLE 5. Average contribution of BLDP and all Skeena sockeye (in parentheses) to the Canadian and Alaskan fisheries and to the spawning escapement, for the periods 1958–71 and 1973–85.

Fisheries and escapements	1000's of Fish				Magnitude of Increase (*x*)
	Pre-BLDP (1958–71)		BLDP (1973–85)		
Alaska Fishery	20.0	(77.3)	85.5	(151.6)	4.3
Canada Fisheries					
Area 3 X, 3 Y	20.4	(82.2)	95.1	(161.9)	4.7
Area 4	144.5	(566.3)	561.1	(1031.0)	3.9
Native Food Fishery	27.5	(44.7)	84.1	(125.0)	3.1
Escapement	146.0	(673.6)	533.8	(983.4)	3.7
Total	358.4	(1 444.1)	1 359.6	(2 452.9)	3.8

Fishery managers are at present coping with this harvesting problem by maintaining low exploitation rates on non-enhanced stocks. Thus, an average annual escapement surplus to spawning needs of the BLDP (369 000) of 165 000 reflects managements efforts to protect other stocks and species. Exploitation of the Pinkut stock has been reduced from 45 to 35% since the intense period of 1972–75, and the Fulton stock has been held to 50% exploitation. Fishing closures early in the commercial fishing season provide almost complete protection for the earliest returning stocks.

Maintaining harvest rates below those which the BLDP stocks can sustain, and thus protecting non-enhanced stocks, is an achievable goal. However, the present high rate of production and average over-escapements of 200 000 sockeye to the BLDP, point to the need to examine supplemental upriver harvesting strategies. As previously stated, the present jack sockeye fishery at the Babine Fence could be expanded to include adults of Fulton and Pinkut origin, or a male-only fishery.

Low productivity of even-numbered brood years from the Babine system prompted McDonald and Hume (1984) to suggest a reduction in even-year escapements and a complimentary increase in landings. If returning pink salmon (*O. gorbuscha*) are active predators on sockeye smolts as hypothesized by Ricker (1982) and Peterman (1982), there is an obvious risk in making any significant reductions in escapement, and consequent smolt production from even-year broods. Any depensatory mortality stemming from adult pinks would then be amplified, particularly if the implicated pinks were from the Babine River stock. However, further speculation on this odd–even year hypothesis may be pointless since the inclusion of more recent data dissolves the regression relationships presented by McDonald and Hume (1984).

The BLDP currently contributes a yearly average of 656 200 sockeye worth some $ 5.5 M (landed value — Canadian) to the commercial Canadian fisheries. Total BLDP construction costs of $ 12 M (1965–71 construction years) with annual operating costs of $ 0.65 M and a discount rate of 10% give a benefit: cost ratio of 3.02:1 (E. Blewet, CDFO, Vancouver, per. comm.). This is an outstanding performance for a sockeye salmon enhancement project.

RESEARCH NEEDS

Spawning channels are designed to optimize the spawning and incubation environments and increase the production of viable fry. In both design and operation, the focus of attention has been on the physico-chemical environment and the fact that egg-to-fry survival in the Babine channels has been twice that of the adjoining rivers suggests the importance of improved abiotic conditions. Egg-to-fry survivals vary widely in both channels and rivers at normal operating densities but the source of this variability is unknown. Hydraulic sampling results indicate that major losses occur before the eyed stage. Improving egg-to-fry survival from long term averages of 40–55% to 65–70%, which has been attained a number of times (Fig. 5), is an attractive target for research.

Continued poor knowledge of juvenile sockeye dynamics in the coastal zone *sensu* Parker (1968) relative to adult returns is of particular concern. Babine smolt production has increased from a mean of 31.2 M before inception of the BLDP to 81.8 M afterward, but smolt-to-adult survival has decreased from 5.1 to 3.0% in the corresponding periods. The cause of the decline in post-lacustrine survival is unknown but could be due to compenstory mechanisms within the stocks, e.g. mortality in the river during seaward migration, in the estuary, or further seaward in the coastal zone (Ricker 1962; Peterman 1982).

Changes in ocean productivity could also affect survival (Ricker 1968). We note that returns of Bristol Bay (Alaska) sockeye stocks have increased threefold from some 10 M during the 1970's to about 30 M during the 1980's, with a 60 M return in 1980 being the largest in the past 25 years (Eggers and Rogers 1987). However, factors other than ocean productivity may have contributed to this increase, and there has been no corresponding increase in the return rate of the unenhanced Babine River sockeye or that of the substantial Rivers Inlet stocks on the Central B.C. coast. Therefore, there is no clear evidence of ocean productivity changes affecting the BLDP stocks.

Finally, the Babine lake spawner assemblage requires critical examination. Surveys (McDonald 1963 and 1964) revealed lake spawners in some Babine Lake areas, prompting the Skeena Salmon Management Committee to identify assessment of lake fry production as a high priority information need for fisheries management. At present, lake spawner estimates are derived from numerical differences between the total stock counts at the Babine Fence and the summed escapement estimates for the BLDP, Babine River, and small tributary streams. Thus, the estimates include all uncounted surplusses of the BLDP which might be forced to spawn in sub-optimal areas, *bona fide* lake spawners, lake mortalities of diverse Babine origin, and errors in estimating escapements to the unenhanced streams. Hence, this lake spawning assemblage is an accounting convenience of unknown reproductive significance.

The number of sockeye categorized as lake spawners has increased from an average of 142 000 (1951–71) to 305 000 (1973–85), peaking at 732 000 in 1985. The increasing size of this assemblage is added cause for concern. By assigning a reproductive success of 233 fry/spawner as for stream spawning populations we would greatly increase estimates of fry inputs to the main lake in recent years. However, if the majority of these adults originate in the BLDP and are therefore surplus to spawning needs there, and are of little reproductive consequence elsewhere in the system, they would constitute a harvestable surplus of considerable interest to fisheries management and industry alike.

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Appendix I

Regression statistics for fecundity on post-orbit hypural length (mm) of Fulton River sockeye for 12 years of return, 1964-85. * = $P<0.05$, ** = $P<0.025$, *** = $P<0.01$, **** = $P<0.005$, ***** = $P<0.001$, NS — not significant.

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1964	4.2	2948	−2290.4 + 11.74	87.7	14	0.75	****
	5.2	3406	−1741.0 + 3.39	103.2	11	0.17	NS
1965	4.2	2657	−1572.3 + 9.86	73.1	12	0.52	NS
	5.2	3320	−899.7 + 8.88	74.7	16	0.61	**
1966	4.2	3186	−754.6 + 5.39	61.9	21	0.42	NS
	5.2	3810	−519.4 + 8.61	103.9	9	0.58	NS
1974	4.2	2937	−692.1 + 8.22	50.9	48	0.45	****
	5.2	3717	−853.2 + 9.10	108.5	26	0.27	NS
1975	4.2	3002	−1006.1 + 8.72	59.9	47	0.41	****
	5.2	3728	−932.0 + 9.16	99.0	29	0.41	*

Appendix I. (Continued)

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1977	4.2	3069	−3383.9 + 13.73	48.3	71	0.62	*****
	5.2	3685	−4269.9 + 15.27	86.1	25	0.61	****
1978	4.2	3185	−1685.4 + 10.77	70.6	21	0.60	****
	5.2	4056	−4973.8 + 1.81	83.2	27	0.11	NS
1979	4.2	3216	−1714.3 + 10.82	65.8	41	0.54	*****
	5.2	4531			1		
1980	4.2	3046	−2038.0 + 11.41	67.5	24	0.61	****
	5.2	3526	−2491.7 + 12.52	55.1	36	0.77	*****
1982	4.2	2720	−3388.2 + 14.16	70.7	29	0.74	*****
	5.2	3470	−621.9 + 8.42	57.8	43	0.50	*****
1983	4.2	2875	−1434.7 + 10.10	73.9	25	0.44	*
	5.2	3476	−2098.7 + 11.79	48.4	40	0.80	*****
1984	4.2	2965	−2481.8 + 12.41	44.7	29	0.66	*****
	5.2	3479	−246.3 + 7.54	60.4	32	0.42	*
1985	4.2	2363	−155.6 + 5.95	62.0	22	0.34	NS
	5.2	3288	−2341.7 + 11.60	50.5	35	0.63	*****
Pooled	4.2	2972	−1811.9 + 10.67	19.1	404	0.59	*****
	5.2	3568	−1244.7 + 9.77	23.1	330	0.56	*****
	4.2+5.2	3240	−2152.0 + 11.52	14.9	734	0.71	*****

Appendix II

Regression statistics for fecundity on post-orbit hypural length (mm) of Pinkut Creek sockeye for 9 yr of return, period 1966–85. Symbols as in Appendix I.

Year	Age	Mean fecundity	Regression $a + b$	s_{yx}	n	r	P
1966	4.2	2897	−2681.7 + 12.82	68.8	23	0.53	***
	5.2	3355	−519.0 + 5.72	147.8	5	0.30	NS
1974	4.2	2970	−1786.6 + 10.52	49.7	25	0.61	****
	5.2	3622	−5263.5 − 3.23	86.4	6	0.44	NS
1975	4.2	2929	−5842.7 + 20.42	61.6	30	0.80	*****
	5.2	3466	−2028.9 + 2.99	121.1	15	0.11	NS
1976	4.2	2932	−3787.8 + 15.22	52.6	39	0.61	*****
	5.2	3274	−3871.3 + 14.66	114.5	10	0.76	**
1977	4.2	3233	−1792.0 + 11.18	49.6	33	0.68	*****
	5.2	3605	−934.7 + 9.08	65.0	31	0.48	***
1979	4.2	3080	−1906.7 + 11.44	90.8	31	0.42	**
	5.2	3864	−6301.4 + 20.33	199.8	3	0.83	NS
1982	4.2	2542	−3119.5 + 13.24	84.6	16	0.63	***
	5.2	3358	−1640.6 + 10.28	52.6	61	0.64	*****
1984	4.2	2333	−1608.5 + 9.53	81.4	19	0.59	****
	5.2	2710	−952.1 + 7.78	83.3	24	0.41	*
1985	4.2	2422	−5046.2 + 17.63	44.1	26	0.80	*****
	5.2	3296	−641.2 + 8.24	54.0	34	0.44	***
Pooled	4.2	2865	−3793.0 + 15.28	24.2	242	0.68	*****
	5.2	3326	−2013.5 + 10.99	30.7	189	0.58	*****
	4.2+5.2	3067	−2015.8 + 11.10	19.5	431	0.69	*****

Development and Evaluation of a Streamside Sockeye Salmon (*Oncorhynchus nerka*) Incubation Facility, Gulkana River, Alaska

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Abstract

ROBERSON, K., AND R. R. HOLDER. 1987. Development and evaluation of a streamside sockeye salmon (*Oncorhynchus nerka*) incubation facility, Gulkana River, Alaska, p. 191–197. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Demand for salmon of the Copper River system has exceeded natural production for a number of years and has resulted in increased conflict among user groups. At the same time, many large lakes in the watershed are underutilized owing to insufficient spawning stock. To increase salmon fry production for an outplant program to the lakes, streamside incubators were installed in 1973 on a high quality spring water source located on the Gulkana River. Incubation capacity of the facility has expanded from 225 thousand eggs in 1973 to 30 million eggs in 1985 making Gulkana the largest such facility in the world. Hatchery fry releases have increased from 200 thousand in 1974 to over 19 million in 1985. Studies are underway to optimize the design of incubators, egg loading densities, procedures for controlling disease, and fry stocking levels in selected nursery lakes.

Current harvest techniques and locations are insufficient to fully utilize the production from enhanced stocks. Coded wire tagging data is used to resolve questions of timing and harvest proportions. Gear types, fishing methods, harvest areas, and fishing categories (sport, subsistence, personal use, and commercial) may all require adjustment.

Résumé

ROBERSON, K., AND R. R. HOLDER. 1987. Development and evaluation of a streamside sockeye salmon (*Oncorhynchus nerka*) incubation facility, Gulkana River, Alaska, p. 191–197. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Pendant un certain nombre d'années, la demande de saumon du réseau hydrographique de la rivière Copper a dépassé la production naturelle, ce qui a eu pour résultat d'envenimer le conflit entre les groupes d'utilisateurs. Au même moment, un grand nombre de lacs importants dans le bassin versant sont sous-exploités en raison d'un stock insuffisant de géniteurs. Afin d'accroitre la production d'alevins de saumon nerka dans le cadre d'un programme d'élevage extérieur, on a installé, en 1973, des incubateurs le long d'une source d'eau vive de très bonne qualité située sur la rivière Gulkana. La capacité d'incubation de l'installation a augmenté, passant de 225 000 oeufs en 1973 à 30 millions d'oeufs en 1985, faisant de Gulkana l'installation du genre la plus grosse au monde. Le nombre d'alevins de pisciculture remis à l'eau a augmenté, passant de 200 000 en 1974 à plus de 19 millions en 1985. Les études se poursuivent pour optimiser la conception des incubateurs, les densités de charge d'oeufs, les procédures pour lutter contre les maladies et contrôler les niveaux d'ensemencement d'alevins dans des lacs choisis servant à la croissance.

Les techniques et les endroits actuels de récolte sont insuffisants pour utiliser au maximum la production des stocks mis en valeur. Des données obtenues à l'aide d'étiquettes métalliques codées sont utilisées pour solutionner les questions touchant le moment de la pêche et les quantités pêchées. Il se peut que l'on doive modifier les types d'engins, les méthodes de pêche, les zones de récolte et le type de pêche (sportive, de subsistance, utilisation personnelle et commerciale).

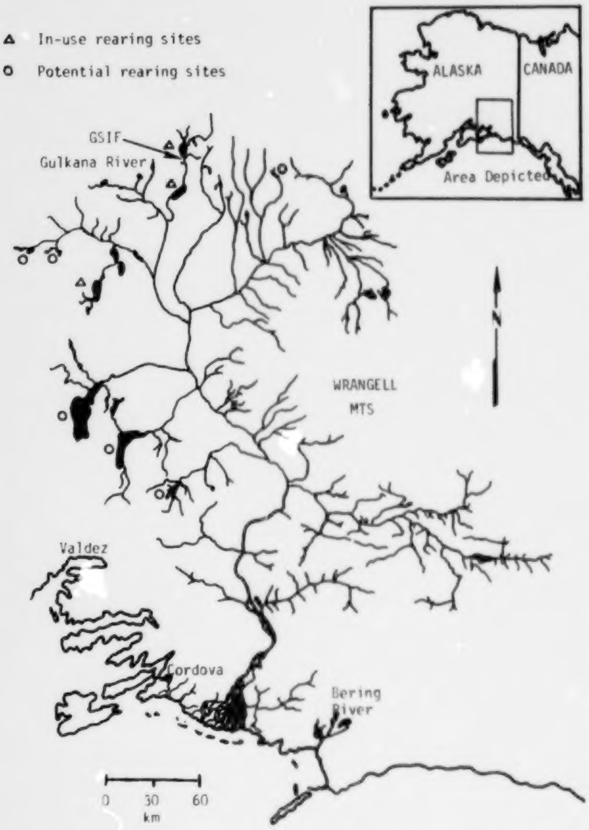

FIG. 1. The Copper River drainage, Alaska showing the location of utilized and non-utilized potential rearing sites.

Introduction

The Gulkana streamside incubation facility is located on the Gulkana River, a major tributary of the Copper River drainage system (Fig. 1). The sockeye salmon (*Oncorhynchus nerka*) of the Copper River are subjected annually to intense commercial, subsistence, and recreational use. Increased demand by numerous user groups in recent years, coupled with a short-term decline in natural salmon production (ADFG 1985), has resulted in conflicts over the available resource. Commercial harvest rates have remained relatively stable over the years and as a result of Limited Entry laws, the number of vessels participating has also remained stable. The increased cost of insurance, gear, and vessels has intensified competition among commercial fishermen and between commercial fishermen and the other user groups. The Subsistence Priority law permits all residents of Alaska to participate in subsistence fisheries and these have priority over commercial fisheries. This law was changed to exclude urban residents in May 1986; however, the subsistence fishery on the Copper River drainage harvested over 100 000 sockeye salmon per season in two recent years while the commercial harvest averages about 650 000 sockeye per season. The present recreational harvest of sockeye is relatively insignificant but that for chinook salmon (*O. tschawytscha*) is increasing and is in direct conflict with the commercial and subsistence harvests of sockeye.

The Gulkana Streamside Incubation Facility (GSIF) for sockeye salmon was constructed in 1973 as a small scale research project. It has been successful from a scientific standpoint and has alleviated some conflicts between user groups by increasing the number of fish available for harvest. The capacity of the GSIF has increased from 225 000 eggs in 1973 to over 30 million eggs in 1985, making it the largest streamside incubation facility for Pacific salmon in the world. The facility has been viewed with some indifference owing to its modest cost and size until the last few years; now that over 25 million eggs are incubated annually at a facility costing approximately $ 50,000 (U.S.) in capital investment, indifference has turned to incredulity. Unfortunately, its success has generated a new set of problems and a need for entirely new objectives. In this paper, we shall describe our approach and results to date, discuss the problems remaining for the Gulkana facility in terms of facility operation and its overall impact on Copper River sockeye stocks.

PROJECT BACKGROUND

The GSIF was designed initially with three major goals: first, to enhance sockeye stocks in the Gulkana River; second, to evaluate streamside incubators as an enhancement technique, and third, to enhance sockeye brood stocks indigenous to warmwater springs located on the Gulkana River for eventual use in a production hatchery.

It was also hoped that the GSIF would mitigate the effects of habitat degradation. Adjacent to the site of the GSIF, there is a floodplain approximately 150 m wide which provides a high quality spawning bed for sockeye salmon. A 10- km reach of river near the GSIF was first narrowed by a wagon trail in the early 1900's, and later by construction of the Richardson Highway, such that by 1964, one third to one half of the available floodplain was lost as spawning habitat.

Due to funding constraints, only a low cost, maintenance free system could be considered for the Gulkana site. The gravity fed streamside incubator concept originally developed by the Canada Department of Fisheries and Oceans (Bams 1970), had already been adapted for use near Cordova, Alaska by ADFG, Commercial Fisheries Division who built and installed several incubators to produce pink salmon fry and they survived well. A new incubator was designed, and a site was selected on the Gulkana River, in consultation with the National Marine Fisheries Service and ADFG staff engineers. Water temperature and chemistry was monitored for one year prior to installing the pilot incubator.

STUDY AREA AND WATER SUPPLY

The GSIF is located about 416 km upstream from the mouth of the Copper River at an elevation of 921 m. The site is located at 63°4′N Lat. 145° 30′W Long., is accessible by highway, and lies between two large oligotrophic lakes near the headwaters of the Gulkana River (Fig. 1 and 2).

The natural spring adjacent to the site provides water of exceptional quality and constant temperature. About 1 km of remnant glacial moraine from the nearby Gulkana Glacier separates Summit Lake (Fig. 2) from the Gulkana River at the site. Hydraulic pressure forces Summit Lake waters through porous zones in the moraine causing springs to vent

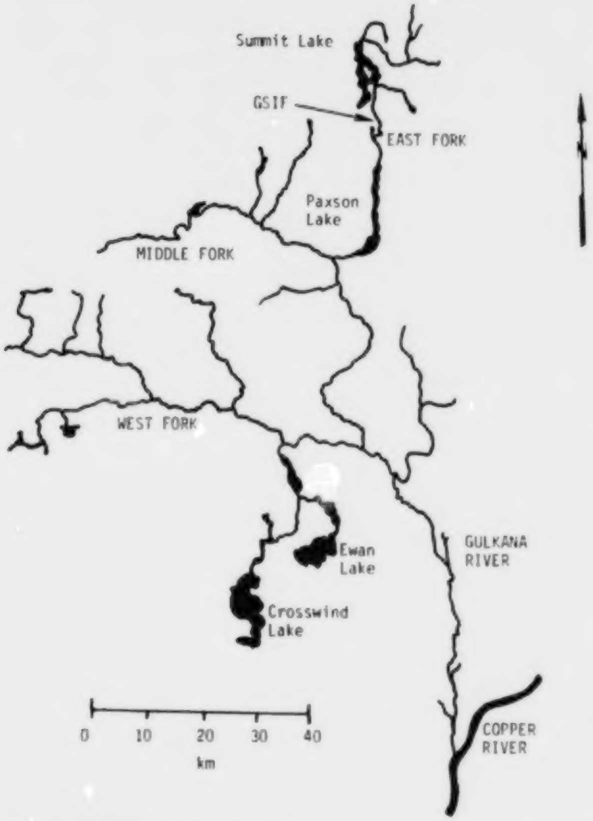
Summit Lake
GSIF
EAST FORK
Paxson Lake
MIDDLE FORK
WEST FORK
Ewan Lake
Crosswind Lake
GULKANA RIVER
COPPER RIVER
0
10
20
30
40
km

FIG. 2. Gulkana River drainage.

along the riverbank. Water at maximum density (3.9°C) is transported through the moraine so the annual flow of the spring at the GSIF varies by less than 10% and water temperature remains between 2.5 and 5.5°C, influenced primarily by air temperature and wind. Water temperature remained within this range even when air temperatures fell to −51°C and wind speeds were at 15–25 kt.

Materials and Methods

INCUBATOR DESIGN, CONSTRUCTION, INSTALLATION, AND MAINTENANCE

Gulkana streamside incubators operate by having water flow upwards through a gravel substrate supporting the eggs (Fig. 3). Fertilized eggs are placed on top of the substrate and remain undisturbed until the alevins burrow into the substrate. Free-swimming fry leave the incubator at their own volition.

Incubators measure 2.44 m × 1.22 m × 1.22 m, are constructed of 1.9 cm AC plywood and have a false bottom, located 12 cm above the base and perforated with 6.4 mm holes on 31.8 mm centers. Water intake lines are 5.1 cm (I.D.) polyethylene pipe; drains and outlets are 7.7 cm (I.D.) ABS pipe. Units are supported on 5 × 15 cm planed lumber structures and fastened with galvanized nails. Lids are constructed from the same materials.

Flow to each incubator is supplied through an independent polyethylene line with at least 1.22 m of effective head originating from 1.22 m × 0.61 m × 0.61 m intake boxes constructed with a pattern of holes corresponding to that of the false bottom described above. Each intake box supplies five water lines which extend 60 to 100 m through the streambed or adjacent ground, and provide flows of 96 L/min in each unit.

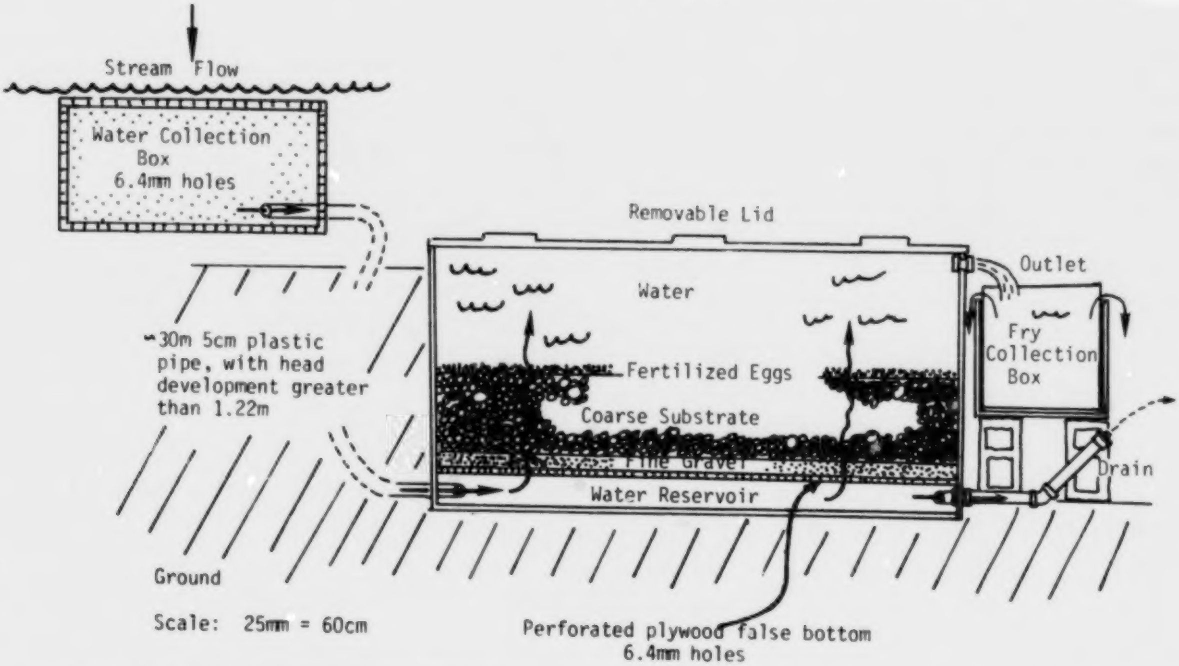
Stream Flow
Water Collection Box
6.4mm holes
Removable Lid
Outlet
Water
Fry Collection Box
~30m 5cm plastic pipe, with head development greater than 1.22m
Fertilized Eggs
Coarse Substrate
Fine Gravel
Water Reservoir
Drain
Ground
Scale: 25mm = 60cm
Perforated plywood false bottom
6.4mm holes

FIG. 3. Reinforced-plywood upwelling incubation unit in use at the Gulkana Streamside Incubation Facility (GSIF).

Each incubator has a 7.6 cm layer of pea gravel (diameter ≤1.27 cm) over the false bottom to filter incoming water, prevent fry from migrating downward, and to distribute flow evenly within the incubator. The coarse substrate, which is placed over the pea gravel to a depth of 30.5 cm is 1.9–3.8 cm graded, smooth river-run gravel. Angular gravel (crushed) and plastic Intalox saddles have also been used experimentally.

Incubators are disinfected annually with household bleach. All substrate is removed and cleaned using industrial cement mixers.

EGG COLLECTION AND INCUBATION

Eggs are usually collected from spawners that congregate in a natural pool within 100 m of the incubation facility. The following egg-take procedures are adapted from those described by McNeil and Bailey (1975). Each fish and all spawn-taking equipment are disinfected with a 200 ppm iodophore solution. Female sockeye are killed with a knife cut which severs the spinal cord and dorsal artery. Female sockeye are kept horizontal and with the belly up to prevent egg loss, and allow blood to drain. Eggs from two females are combined and fertilized simultaneously with milt from two males using standard techniques. Fertilized eggs are rinsed and then water hardened in a buffered 100 ppm iodophore solution in an attempt to eliminate the IHN virus. Water-hardened eggs are pooled, enumerated volumetrically, and loaded into incubators at a rate of 0.5 million per unit.

The loaded incubators receive no maintenance or operational adjustments except for monthly treatments with a fungicide (malachite) using a modified California flush technique. During treatment, each unit is partially drained to remove detritus which accumulates under the false bottom of the incubators. Routine chemical analyses are also performed on the water supply (DO, pH, etc.) to ensure that desired water quality standards do not deteriorate. The incubators are usually covered by as much as 1 m of snow with only their outlet end visible during most of the incubation period. Ice commonly forms around the incubator outlets and fry collection boxes during extended periods of −10° C or colder but does not interfere with incubator operation. A Ryan J90 recording thermograph provides a record of temperature fluctuations in the water supply.

FRY EMERGENCE

Production data are recorded for individual incubators to evaluate the influence of loading density, substrate, disinfection and other procedures on egg-to-fry survival. Each incubator has an impervious plywood fry collection box under the outlet. It has an aluminum screen liner which collects fry for enumeration. Fry enumeration procedures have been modified as production increased. Fry were enumerated with hand counters when abundance was low. At higher abundance, volumetric sampling was used for fry numbers up to about 12 000 and total weight was used for numbers above that. Beginning in 1985, Northwest Marine Technology Inc. FC 1 counters were used to count fry samples from each individual incubator.

Fry samples are collected from all incubators when each of 25%, 50%, and 75% cumulative emergence totals are expected. Changes in developmental indices (KD, Bams 1970) are calculated and compared with those of fry from natural spawning sites.

Approximately five million fry were released into the river at the GSIF from 1982–86 to provide sufficient brood stocks for the next generation. The remainder were transported by highway vehicle or aircraft to lakes selected on the basis of estimated carrying capacity and transportation cost. Fry are transported in a 0.28 m³ capacity mobile tank, or in 50-L Nalgene bottles supplied with oxygen. Fry are acclimated to within 2°C of ambient temperature in the nursery lake before release.

CODED-WIRE TAGGING STUDIES

Natural production in Summit Lake is probably very low since the spawning population averages < 100 adults; however, it receives a major portion of the recent fry production from the GSIF. Since 1981, some of the smolts emigrating from Summit Lake have been tagged using a Northwest Marine Technology Inc. coded-wire tagging machine. Smolts are captured in a 93-m net placed in a low velocity zone of the lake outlet, enumerated, and sampled for age, length, and weight and then tagged. Adipose fins were removed from each fish tagged.

Tagging in 1981 was conducted primarily to test procedures and although less than 1 500 smolts were tagged, one was recovered as an adult in an ADFG spawing area recovery program in 1984. Beginning in 1982, approximately 20 000 smolts were tagged annually. In 1984 and 1985, approximately 30% of the commercial fishery catches were sampled, almost exclusively in processing plants in Cordova where the vast majority of Copper River salmon are processed.

ADULT SALMON INVESTIGATIONS

Adult salmon returns have been assessed using aerial surveys from fixed wing aircraft, weir counts, and spawning ground surveys.

LIMNOLOGICAL INVESTIGATIONS

Major limnological investigations began in 1980 on Paxson and Summit lakes (Fig. 2). Since then, nearly every lake in the entire Copper River drainage that appeared to have rearing potential for juvenile salmon has been surveyed. Zooplankton, periphyton, phytoplankton, particulate nutrients, temperature, pH and DO stratification, light penetration, ice thickness, and related parameters have been recorded. Bathymetric maps have been prepared and general chemical analysis has been done for each lake. Sampling methods and procedures were as outlined by Koenings et al. (1980).

FISH PATHOLOGY STUDIES

The principal disease threat to the enhanced stock is Infectious Hematopoietic Necrosis (IHN). Samples of GSIF fry have been examined histologically each year from 1973. In addition, ovarian fluid samples have been collected and analyzed each year from 1976. These samples were examined by the ADFG, FRED Division Pathology Laboratory in Anchorage using a plaque assay technique. Both the percent of adults infected and a viral titer for individual fish were determined.

Results

EGG TAKE AND INCUBATION

Incubators in use at GSIF have proven inexpensive to assemble and install. Moreover, they provide adequate insulation against cold temperatures at Gulkana and can be readily destroyed if contaminated by IHN.

Because eggs are not handled after placement in the incubators the quality of the egg take largely determines survival to the fry stage. Survival from green egg to emergent fry has consistently approached or exceeded 80% when full care has been exercised but fell to 50–55% when rigorous procedures were not followed (Roberson and Holder 1984). We consider the care taken at the GSIF to be among the most rigorous for salmon anywhere.

Originally, incubators were loaded with 200 000 - 300 000 eggs (0.23–0.35 eggs/cm^3 of substrate). Loading densities were increased over a period of several years without a significant loss in fry quality until densities exceeded 600 000 eggs per incubator (0.70 eggs/cm^3 of substrate). Above this, premature fry emergence occurred even though survival rates remained at 80–90%. A standard of 500 000 eggs per incubator was established in 1982. Since that time survival rate and the average size of emerging fry has ranged from 80 to 91%, and 27.3 to 27.7 mm, respectively.

Mean fecundity for Gulkana River sockeye is approximately 3 980 (Roberson and Fridgen 1974) whereas effective fecundity during the egg take drops below 3 400 (Roberson and Holder 1984) because of egg retention or the inadvertent inclusion of some partially spawned or green females.

FRY EMERGENCE

The survival and quality of emergent fry from various substrates at the GSIF have been compared with naturally incubated fry and reported by Holder (1986); these results are summarized briefly as follows: The substrates tested in the incubators were rounded river gravel, fractured and crushed river gravel, and plastic Intalox saddles. Median emergent timing for fry was significantly different between the three hatchery substrates. GSIF fry survival was 4.25 times that of natural fry. Facility fry were shorter and lighter and emerged at an earlier stage of development (equal to 3.4 -13.4 days growth), but had median times of emergence 9.6, 11.7, and 13.3 days later than natural fry from round, angular, and plastic substrates, respectively. Apparently, GSIF alevins developed at different rates in different substrates.

CODED-WIRE TAGGING STUDIES

Approximately 20 000 coded wire tags have been applied to smolt from Summit Lake annually, 1982–86. Attempts to enumerate entire smolt outmigrations with nets were unsuccessful because ice or algae mats entered the nets and either damaged them, or prevented fishing the whole river channel. Outmigrant smolts were nearly all age 1, with a mean length of 92 mm and range from 82 to 106 mm. In 1986 a significant decline in length (sample means, 76–83 mm) occurred which is attributed to increased population densities. Fry stocking densities have increased by 630% since 1980 and are now at approximately 50% of the estimated carrying capacity.

Recovery of significant numbers (46 and 76 in 1985 and 1986, respectively) of Gulkana tags in the Copper River commercial fishery zone demonstrates that GSIF fish are surviving and contributing to the total return of Copper River sockeye. Expansion of tag ratios from Summit Lake returns suggests that smolt-to-adult survival is about 1%. However, mark:unmark ratios were lower than expected so this estimate is probably too low. The mark:unmark ratios of coded wire tags or adipose fin clips among adults returning to Summit Lake was only 1:50.5 compared with 1:26 expected on the basis of smolt estimates and the number of marks applied. Tag loss, adipose fin regeneration, or underestimated smolt numbers may explain the lower than expected ratios. Tag recovery spans the entire sockeye fishing season from mid-May through the end of July and suggest a broader run timing pattern than was indicated by historical tagging studies. Future runs should permit us to address these matters more fully.

ADULT SALMON INVESTIGATIONS

Aerial and ground survey estimates, and weir counts of returning adults on streams and lakes that receive GSIF fry have consistently demonstrated that about one percent of the fry released return as adults. Returns as early as 1978 to the release site on Ten Mile Lake, which was barren of sockeye prior to fry introductions in 1974, demonstrated survivals about as expected (annual releases of 100 000 fry in 1974–76 resulted in 250–925 adults according to ground and aerial estimates; see Table 1). Recent trends in returns to Summit Lake and the incubation facility demonstrate increases in abundance for which returns from GSIF fry releases are the only tenable explanation (1.86 million fry released to Summit Lake in 1981 produced an estimate of 4 180 adults in the escapement alone; Table 1). Although historical spawning escapements at this site seldom exceeded 1 500 fish, recent spawning escapements have probably exceeded 20 000 (Table 1).

LIMNOLOGICAL INVESTIGATIONS

Lakes with a combined surface area of over 31 000 ha have been identified as potential rearing areas for facility fry. Approximately $1\ 250 \times 10^6$ m^3 of euphotic zone are included in the lakes indicated above, thus signifying a very large potential for increased sockeye production in the watershed.

FISH PATHOLOGY STUDIES

IHN virus has been found in 27–98% of returning adults with significant numbers of females showing ovarian titers exceeding 10^5 plaque-forming units. In 1983, 1984, and 1985, emerging fry in some incubators showed signs of IHN

TABLE 1. Production data from the Gulkana Streamside Incubation facility (GSIF).

Brood year	Fry release site	Fry release	Estimated commerical catch	Estimated escapement
1973	GSIF	79 700	320[h]	500[g]
	Ten Mile Lake	99 600	400[c]	800[a]
1974	GSIF	785 100	1 600[h]	2 500[g]
	Ten Mile Lake	101 400	200[c]	925[a]
1975	GSIF	626 000	1 200[h]	4 000[g]
	Ten Mile Lake	101 600	200[c]	250[a]
1976	GSIF	516 300	3 000[h]	4 500[g]
	Ten Mile Lake	112 200	600[c]	150[a]
1977	GSIF	479 000	3 000[h]	5 300[g]
	Ten Mile Lake	104 100	600[c]	440[a]
1978	GSIF	940 700	6 000[h]	6 500[g]
	Ten Mile Lake	99 600	600[c]	—[b,a]
1979	GSIF	1 105 400	4 054[e]	13 700[g]
	Summit Lake	1 340 100	4 944[d]	950[a]
1980	GSIF	3 388 700	21 790[e]	16 500[g]
	Summit Lake	1 860 500	7 619[d]	4 180[a]
1981	GSIF	5 985 300	22 721[e]	19 000[g]
	Summit Lake	2 047 947	7 781[d]	1 975[a]

[a] Aerial survey data.

[b] Major blockage by beaver dams.

[c] Significant fishery closures during migration period.

[d] Based upon coded wire tag recovery rate.

[e] Assumes same exploitation rate as for CWT group.

[f] Average escapement to GSIF spring prior to facility development was 1 500 spawners.

[g] Number used for egg take; in excess of the 1 500 assumed to be from natural production and needed for natural seeding.

[h] Interpolated from relative fry production.

and these were confirmed by laboratory tests. All affected fish and incubators were destroyed. The overall mortality due to IHN was 4% of the total egg take at the facility in those years.

Discussion and Conclusions

Preliminary assessments of the GSIF show that its three major goals are being met, but a more definitive appraisal must await the analysis of additional tag recoveries in both the catch and spawning escapement. The facility and operations have proven reliable and a brood stock capable of providing an egg quota of 30 million has been developed without adversely affecting the natural spawning population of sockeye. Operational costs for the facility (including evaluation) are extremly low ($266,000 in fiscal year 1986) compared to other facilities of similar capacity. Two other Alaskan facilities each with a capacity for 20 million eggs have annual operational costs averaging about $375,000, not including evaluation. IHN infection is being effectively controlled through disinfection and incubator isolation. Numerous large lakes which are either under- or non-utilized by anadromous salmon have been identified as potential rearing areas and a second facility is being considered for a site only 6 km from the GSIF. This would be larger (50 million eggs capacity) and designed to produce sockeye and chinook, and possibly other species of salmon.

Thus the largest and probably most cost efficient sockeye incubation facility in the world may appear to have few obstacles to future success and able to reduce both user-group demands and competition. The question is: are these expectations realistic, or will the expansion program simply exacerbate existing resource management problems?

Nearly 100 sockeye stocks, including the GSIF stock, and 38 chinook stocks occur together in most, if not all, of the significant fisheries of the Copper River, including catches made by the various commercial, subsistence, and personal use fisheries from tidewater to points far up the Copper River system. This demanding and complex pattern of use together with the large increase in returns from an enhanced stock that could withstand a commercial harvest rate 20–25% in excess of natural stocks, creates enormous difficulty for the fishery manager. There are, of course, many instances in which natural production has suffered from increased exploitation rates required to effectively harvest more productive enhanced stocks (Oregon coho, Puget Sound chinook, Columbia River chinook, and certainly Pacific Coast chinook and coho in general, all have such management problems). However, mixed stock problems have also occurred in the absence of enhancement when effective harvest of productive wild stocks has decimated less productive ones. Comprehensive management planning should place the collective natural stocks as the sole priority and allow harvest of any excess available from either natural or enhanced stocks at locations, times, and by methods which minimize potential conflicts. It must be acknowledged that the high benefit to cost ratio of this enhanced stock population allows utilization at much lower rates than for most facilities.

Clearly future enhancement projects must be considered carefully with respect to species selected, release sites, timing of stocks in the fisheries, and acceptable harvest scenarios. Without those even the most cost-effective and biologically productive enhancement project may be doomed to failure due to logistic difficulties and political disputes — a failure for which resource managers could take full blame.

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Lake Fertilization: The Enrichment Cycle and Lake Sockeye Salmon (*Oncorhynchus nerka*) Production

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Abstract

STOCKNER, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production, p. 198–215. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The sockeye nursery lakes of British Columbia are broadly classified as either monomictic coastal or dimictic interior. They are further separated by water transparency into humic-stained (dystrophic), clear, and glacial systems. Primary production rates are exceedingly low in glacial systems (ultra-oligotrophic), slightly higher in coastal clear and dystrophic lakes (oligotrophic), and considerably higher in interior lakes (oligo-mesotrophic). Picoplankton and small nanoplankton are responsible for most carbon production in all coastal and glacial systems. Primary production shows a sequential increase following weekly fertilizer application to surface waters, peaking the third day after application. Increased primary production resulting from whole-lake fertilization depends on weekly loading rates, but averages about 2 to 2.5 × pretreatment values. Phosphorus input–output budgets from Great Central and Bonilla lakes are compared with published P-budgets from other well-studied sockeye lakes. Fluvial inputs are primary sources of phosphorus to all lakes, but biogenic inputs from adult carcasses can also be a significant contribution to the annual total phosphorus input. Outmigrant smolts remove only a small fraction of phosphorus from the lakes, with the majority being retained and lost to deep-water sediments. Phytoplankton carbon size-spectra for coastal lakes reflect the oligotrophic condition and show marked increases in carbon with treatment without changes in particle-size distribution. Zooplankton abundance affects quantity and quality of size-spectra, and is related to pelagic planktivorous fish density. Trophic pathways leading to juvenile sockeye are presented and potential energy sinks that dissipate energy are identified and discussed. Pelagic fish standing stocks in coastal lakes are estimated to be very low and are related to average lake total phosphorus content.

Résumé

STOCKNER, J. G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production, p. 198–215. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les lacs d'alevinage de saumon nerka de la Colombie-Britanique sont classés en deux grandes catégories : côtier monomictique ou intérieur dimictique. Ils sont ensuite répartis selon la transparence de l'eau en systèmes colorés d'acide humique (dystrophe), glaciaires et à eau claire. Les taux de production primaire sont extrêment faibles dans les systèmes glaciaires (ultra-oligotrophes), légèrement plus élevés dans les systèmes côtiers à eau claire et les lacs distrophes (oligotrophes) et beaucoup plus élevés dans les lacs intérieurs (oligo-mésotrophes). Le picoplancton et le petit nanoplancton sont les principaux producteurs de carbone dans tous les systèmes côtiers et glaciaires. La production primaire montre une augmentation séquentielle suite à l'application hebdomadaire de fertilisants dans les eaux superficielles; elle atteint une pointe trois jours après l'application. Une production primaire accentuée par la fertilisation complète d'un lac dépend des taux de charge hebdomadaires; elle varie en moyenne de 2 à 2,5 fois les valeurs observées avant le traitement. On compare les bilans du phosphore à l'entrée et à la sortie des lacs Great Central et Bonilla avec les bilans relevés dans les ouvrages publiés sur d'autres lacs fréquentés par le saumon nerka. Les apports fluviaux sont les principales sources de phosphore dans tous les lacs, mais des apports biogéniques provenant de carcasses d'adultes peuvent représenter une contribution importante au bilan annuel de phosphore total. Les smolts dévalants n'enlèvent qu'une petite partie du phosphore la custre quoique la plus grande partie soit retenue dans les sédiments en eaux profondes. Les spectres de taille du carbone chez le phytoplancton présent dans les lacs côtiers traduisent leur état oligotrophe et révèlent des augmentations marquées du carbone suite au traitement sans une variation coïncidente de la distribution de la taille des particules. L'abondance du zooplancton influe sur la qualité et la quantité des spectres de taille et est liée à la densité des poissons pélagiques planctivores. On présente les cheminements trophiques jusqu'au saumon nerka juvénile et on examine les pièges potentiels d'énergie qui la dissipent. La biomasse des poissons pélagiques dans les lacs côtiers est considérée très faible et en relation avec la teneur moyenne de phosphore lacustre total.

Introduction

> "Since the production of zooplankton depends on the abundance of phytoplankton and this, in turn, on the quantities of inorganic substances and on favorable conditions for rapid and extensive photosynthesis, a thorough study of primary production in sockeye producing lakes is of paramount importance. Despite its importance, however, in the consideration and evaluation of a lake as a food-producing unit for young sockeye and its intimate role in the food-chain, phytoplankton production has been, thus far, but cursorily studied in sockeye lakes."
>
> R. E. Foerster, *The Sockeye Salmon*. 1968, p. 205–206, p. 211.

Since the period of the last major glaciation, some 12 000–15 000 years B. P., the many lakes, and tributary streams of lakes, of Pacific coastal regions of North America and Asia have been successfully utilized by anadromous sockeye salmon (*Oncorhynchus nerka*). With the exception of a few races of sockeye that have adapted to riverine and early estuarine rearing, most populations have evolved a very specific requirement for lacustrine rearing by developing a planktivorous feeding habit. After emergence, early fry may utilize lake littoral habitat (Mathisen 1966, 1972), but soon the majority move offshore and become pelagic zone feeders.

The seasonal productivity of many sockeye nursery lakes appears to be dependent upon the autumn and early winter input of nutrients from adult carcasses (Donaldson 1966), and detailed records by several early investigators have suggested a strong correlation between numbers of returning adults and subsequent lake productivity (Gilbert and Rich 1927; Juday et al. 1932; Krogius and Krokhin 1956). However, there are few limnological studies that have either documented processes or identified variables that may be responsible for enhanced juvenile sockeye growth and survival.

Dramatic reductions in adult returns following the advent of trap and net commercial fisheries for sockeye at the turn of the century led early workers to postulate that nutrient loss to nursery lakes was a consequence of overfishing, and thus proposed lake fertilization as a possible means of restoring depressed populations (Juday et al. 1932). The experimental fertilization of Bare Lake, Alaska demonstrated striking increases in primary and secondary production (Nelson and Edmondson 1955), and a strong relationship between primary production and smolt growth (Nelson 1958). However, failure to assess adult escapements from treated broods cast some doubt on the efficacy of the technique for sockeye enhancement. Not until whole-lake fertilization experiments were begun in Great Central Lake, B.C. in 1970 (Parsons et al. 1972; LeBrasseur et al. 1978), and subsequently shown to be effective for sockeye enhancement in other B.C. coastal systems (Stockner and Hyatt 1984; Hyatt and Stockner 1985), did the technique gain more general acceptance.

The objectives of this report are threefold: first, to review the nature of the phytoplankton production response in both treated and untreated coastal, interior, and glacial British Columbia lakes; second, to present a simple input–output phosphorus budget for Great Central and Bonilla lakes to examine processes responsible for enhancement of the food-resources of juvenile sockeye; and finally, to identify key links and sinks in sockeye nursery lake food-webs, and to discuss possible relations between fertilization, the autotrophic response, and fish growth.

Methods

Experimental methods and analytical procedures used by the limnology unit of the Lake Fertilization Program (LEP), Fisheries Research Branch, West Vancouver Laboratory and Pacific Biological Station, are presented in detail in several recent publications (Stockner et al. 1980; Stockner and Shortreed 1985; Stockner and Hyatt 1984; MacIsaac and Stockner 1985; Hyatt and Stockner 1985). Data presented here from Babine Lake and selected Fraser River lakes were obtained by methods described either by Stockner and Shortreed (1974, 1975, 1983), or by Goodlad et al. (1974). Least squares linear regression analysis was used to determine empirical relationships between collected LEP data (Sokal and Rohlf 1969).

Study Area

THE SOCKEYE LAKES OF BRITISH COLUMBIA

Geographically, the sockeye nursery lakes of B.C. can be broadly categorized as either coastal or interior (Fig. 1). The climate of coastal lakes is strongly influenced by the Pacific Ocean and most are continuously deep mixed during winter and thermally stratified in summer (monomictic). The coastal climate is characterized by cool, wet winters and moderately warm, dry summers on the south coast, and cooler, wetter summers on the north coast. Interior lakes lie on the leeward side of coastal mountains and experience a more

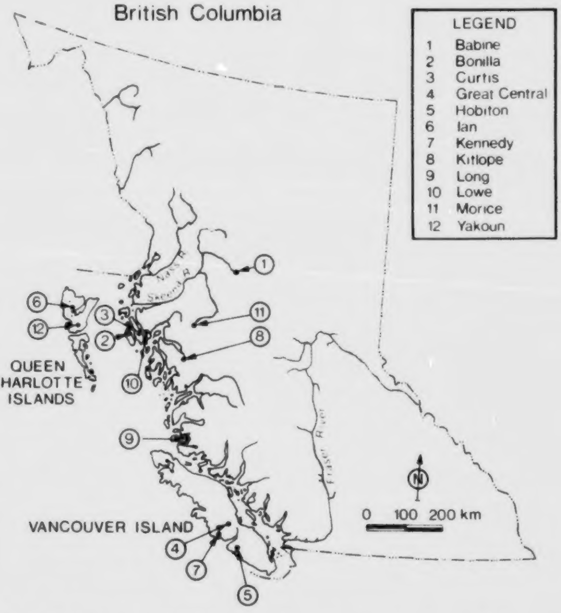


FIG. 1. British Columbia with location of lakes referred to in text.

typically continental climate, and with protracted periods of ice-cover in winter undergo two episodes of mixing, before and after ice-formation and summer and winter stratification (dimictic). These climatic differences impart differing hydrologic cycles that directly influence nutrient inputs, water retention, and seasonal productivity patterns.

Coastal lakes tend to be fast-flushing, experiencing maximum water input and nutrient loads in winter, when light intensities, water temperatures, and water column stability are low. Consequently, nutrient concentrations and base levels of production tend to be very low and the lakes are generally classed as oligotrophic (Parsons et al. 1972; Stockner 1981; Stockner and Shortreed 1985). Interior lakes receive peak flows and nutrient inputs in spring as drainage basin snow melts and ice leaves. At this time light intensity, surface temperature, and water column stability are all rapidly increasing. Interior lakes show strong vernal production peaks (Stockner and Shortreed 1975), and are generally categorized by their higher nutrient and productivity levels as oligo-mesotrophic (Northcote and Larkin 1956; Ward 1957; Stockner and Shortreed 1975, 1983).

When one considers the marked differences in climate, hydrology, water chemistry, and base production levels between typical coastal and interior British Columbia lakes, it is not surprising that there are also differences in the biological communities of these lakes. Numbers of free-living bacteria, phytoplankton, and zooplankton tend to be considerably higher in interior lakes (Table 1) (Stockner and Shortreed 1983). Not only are the standing stocks greater, but species assemblages are generally more diverse at most trophic levels (Goodlad et al. 1974). On average, sockeye smolts leaving interior lakes at age 1 are larger than those from coastal systems, suggesting the inherent higher productivity or greater rearing area of major interior sockeye lakes (Foerster 1968; Goodlad et al. 1974; Johnson 1965; Hyatt and Stockner 1985).

Within the broad category of coastal lakes a further separation can be made on the basis of size, transparency, and average epilimnion temperature and depth. The majority of coastal sockeye lakes from central British Columbia and including the Alaska panhandle tend to be smaller and generally more humic-stained (dystrophic) than many southern Vancouver Island sockeye lakes. Humic substances and other refractory organic materials impart a weak acidity in these dystrophic lakes, and reduce light penetration which diminishes the depth of the euphotic zone. The prevalence of cool, wet, and overcast conditions reduces the length of the growing season, and average epilimnion temperatures tend to be lower (Table 1). Many of the major sockeye lakes of the south coast are larger and have deeper epilimnia, larger euphotic zones, and longer growing seasons (Table 1).

TABLE 1. Average August–September values for selected variables from British Columbian coastal, interior, and glacial sockeye nursery lakes. (*n* = number of observations, F. = Fertilized lake, U = Unfertilized lake).

	Coastal				Interior[c]	Glacial[d]	
	North[a]		South[b]				
Variable	F	U	F	U	U	F	U
Epilimnetic temperature (°C)	15.5 (*n* = 66)	16.2 (*n* = 5)	17.8 (*n* = 115)	18.1 (*n* = 33)	12.7 (*n* = 10)	11.1 (*n* = 15)	—
Compensation depth (m)	5.1 (*n* = 54)	6.0 (*n* = 10)	11.2 (*n* = 76)	15.1 (*n* = 29)	10.1 (*n* = 10)	9.3 (*n* = 16)	8.1 (*n* = 4)
Bacteria numbers (× 10^6 • mL^{-1})	1.45 (*n* = 32)	0.67 (*n* = 3)	1.38 (*n* = 59)	0.74 (*n* = 26)	1.40 (*n* = 5)	1.03 (*n* = 12)	0.68 (*n* = 1)
Phytoplankton volume (mm^3 • m^{-3})	415 (*n* = 31)	173 (*n* = 2)	1973 (*n* = 54)	937 (*n* = 23)	—	304 (*n* = 10)	20 (*n* = 6)
Zooplankton biomass (mg • m^{-3})	27.1 (*n* = 41)	4.8 (*n* = 2)	9.94 (*n* = 46)	4.98 (*n* = 36)	61.3 (*n* = 5)	7.6 (*n* = 14)	12.2 (*n* = 5)
Chlorophyll (µg • L^{-1})	1.99 (*n* = 36)	1.52 (*n* = 2)	2.32 (*n* = 69)	0.95 (*n* = 26)	2.65 (*n* = 10)	1.17 (*n* = 14)	0.60 (*n* = 1)
Primary production (mg C • m^{-2} • d^{-1})	178 (*n* = 12)	66 (*n* = 2)	157.3 (*n* = 21)	70 (*n* = 12)	204 (*n* = 10)	84 (*n* = 6)	60 (*n* = 1)

[a] North: Awun, Ian, Eden, Bonilla (1982), Curtis (1981–82), Devon, Lowe,

[b] South: Kennedy–Clayoquot (1984), Kennedy–Main, Hobiton, Henderson, Nimpkish, Great Central, Sproat, Mohun.

[c] Interior: Babine (1980).

[d] Glacial: Morice, Kitlope.

The glacial lakes form the third category of B.C. sockeye lakes, and include both monomictic coastal and dimictic interior types. Glacial lakes have shallow euphotic zones and cool epilimnetic temperatures and highly variable mixed-layer depths. They are best characterized as ultra-oligotrophic with very low base productivities and standing stocks of bacteria, phytoplankton, and zooplankton (Table 1). Most glacial lakes show turbidity gradients in summer imparted by suspended clays and glacial flour carried by tributary streams, with less turbid regions showing higher productivities and greater plankton densities e.g. Meziadin, Owikeno, Kitlope, Morice and Chilko lakes (Stockner and Shortreed 1978; Shortreed and Stockner 1981; Stockner et al. 1980). Some of the smallest age 1 sockeye smolts come from glacial systems (Hyatt and Stockner 1985; Goodlad et al. 1974; Koenings et al. 1986).

Autotrophic production in the vast majority of British Columbia sockeye lakes appears to be phosphorus (P) limited (Stockner and Shortreed 1975, 1985). However the epilimnia of many coastal systems become deplete of dissolved nitrogen (N) soon after commencement of stratification, and phytoplankton are therefore co-limited by both P and N for much of the growing season (Perrin et al. 1984; Stockner and Shortreed 1985; MacIsaac and Stockner 1985).

Results and Discussion

PRIMARY PRODUCTION

Annual average rates — Lakes representative of the three major types of sockeye nursery lakes show marked differences in average daily primary production rates under treated and untreated conditions (Table 2). Fertilized coastal lakes show large increases in primary production, and the magnitude of response is highly correlated with phosphorus load from fertilizer (P-fert) (Stockner and Shortreed 1985). Fertilized coastal lakes can become more productive than untreated, interior Babine Lake (Table 2). The two glacial systems (Morice and Kitlope lakes) showed low production rates even under fertilized conditions and average production levels were comparable to untreated coastal lakes (Table 2). The efficiency of production or Production/Biomass (P/B) ratio (mg C • mg Chl^{-1} •d^{-1}) also increases with higher fertilizer loading rates. Untreated coastal lakes show less efficient production per unit chlorophyll than untreated interior Babine Lake (Table 2). Primary production data from major Fraser River sockeye lakes were not available for comparison with coastal systems, however, mean values of biological variables (bacteria, chlorophyll, zooplankton), for some major interior lakes (Stuart, Fraser) exceeded Babine Lake (Goodlad et al. 1974; Stockner and Shortreed 1983).

Seasonal patterns — There are few well-defined peaks or troughs in seasonal plots of primary production for untreated coastal or glacial lakes (Fig. 2). In the treated condition both daily and annual production rates are higher (Stockner et al. 1980), with some peaks in the seasonal pattern (Fig. 2). In interior systems, more pronounced spring and often autumn production peaks prevailed (Fig. 2). These differences in seasonal patterns appear related to the hydrologic cycle of coastal lakes, where winter and early spring flushing reduces ambient nutrient concentrations and limits the magnitude of spring phytoplankton responses at the onset of stratification. For example, high primary production rates have been noted in February and early March in monomictic coastal lakes where they are thought to be associated with protracted

TABLE 2. Variation in average daily primary production, chlorophyll, and turnover rates for represent ive British Columbia sockeye nursery lakes (F = Fertilized lake, U = Unfertilized lake).

	Coastal				Interior	Glacial	
	North		South				
	F[a]	U[b]	F[c]	U[d]	U[e]	F[f]	U[g]
Primary production (mg C • m^{-3})	64.1	6.3	31.1	8.2	20.3	8.0	5.2
P-Load, fertilizer (mg P • m^{-2} • wk^{-1})	11.6	—	4.6	—	—	2.9	—
Total chlorophyll (mg • m^{-3})	4.5	1.0	4.0	1.2	1.9	1.0	1.1
P/B (mg C • mg Chl^{-1} • d^{-1})	14.2	6.3	7.8	6.8	10.7	5.0	4.7

[a] Bonilla Lake; 1980, 1981, 1982, 1983.
[b] Bonilla Lake; 1979.
[c] Kennedy Lake, Clayoquot Arm; 1980, 1982, 1983.
[d] Kennedy Lake, Main Arm; 1981, 1982, 1983.
[e] Babine Lake (ave. Stations 1–10); 1973.
[f] Morice Lake (Station 1); 1980.
[g] Morice Lake (Station 2); 1980.

periods of clear, calm weather and water column stability (LEP, unpublished data). These early phytoplankton increases reduce available nutrients and dampen the strength of the vernal response. Glacial lakes tend to stratify late, which minimizes the occurrence of vernal production peaks. The strong vernal production peaks that are often common in interior lakes are the result of higher ambient nutrient concentrations in surface waters. High light intensity, increasing temperatures, and water column stability (stratification) create near optimal conditions for phytoplankton growth at this time.

Autumnal peaks are more common in interior lakes and are related to the thermocline deepening as the epilimnion cools. Frequent storm events and associated episodes of deep-mixing further entrain nutrients from hypolimnetic water (Stockner and Shortreed 1975). One reason coastal systems show less pronounced autumn production peaks than interior lakes is because their hypolimnetic waters are too nutrient depleted to significantly affect primary production when entrained into the epilimnion. For example, in the North Arm of Babine Lake (Stn. 1) just prior to overturn in late September, 1980, hypolimnetic NO_3-N concentrations were 108 µg • L^{-1}, while September NO_3-N values in the hypolimnion (20 m) of coastal Kennedy Lake–Main Arm, 1980 were only 38 µg • L^{-1}; nearly a three-fold difference in NO_3-N to be mixed into similar epilimnetic volumes.

Because of the absence of a strong vernal phytoplankton increase in warm-monomictic coastal lakes, zooplankton often reach peak numbers and biomass as late as mid-August or early September, and timing of sockeye fry recruitment to the pelagic zone tends to be more protracted than in dimictic lakes (T. Gjernes, Pacific Biological Station, Nanaimo, B.C., personal communication). In interior Babine Lake, strong spring phytoplankton increases are followed by zooplankton abundance peaks in mid-June and early July, and sockeye fry recruitment is timed very precisely to coincide with these food increases (Stockner and Shortreed 1975; H. D. Smith, 1090 West Pender St., Vancouver, B. C., personal communication).

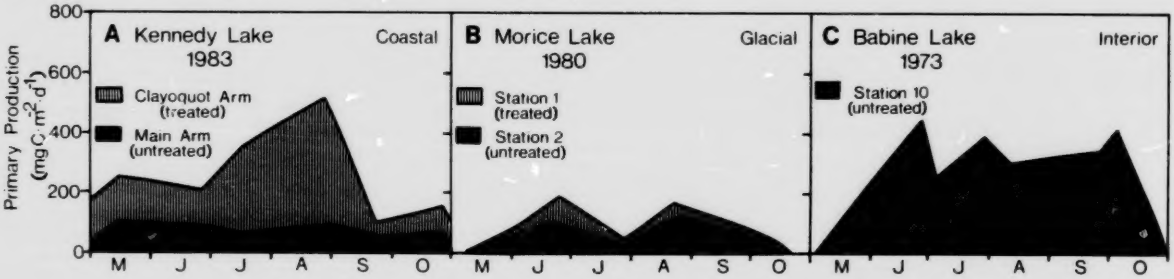


FIG. 2. Seasonal primary productivity of selected B.C. sockeye lakes.

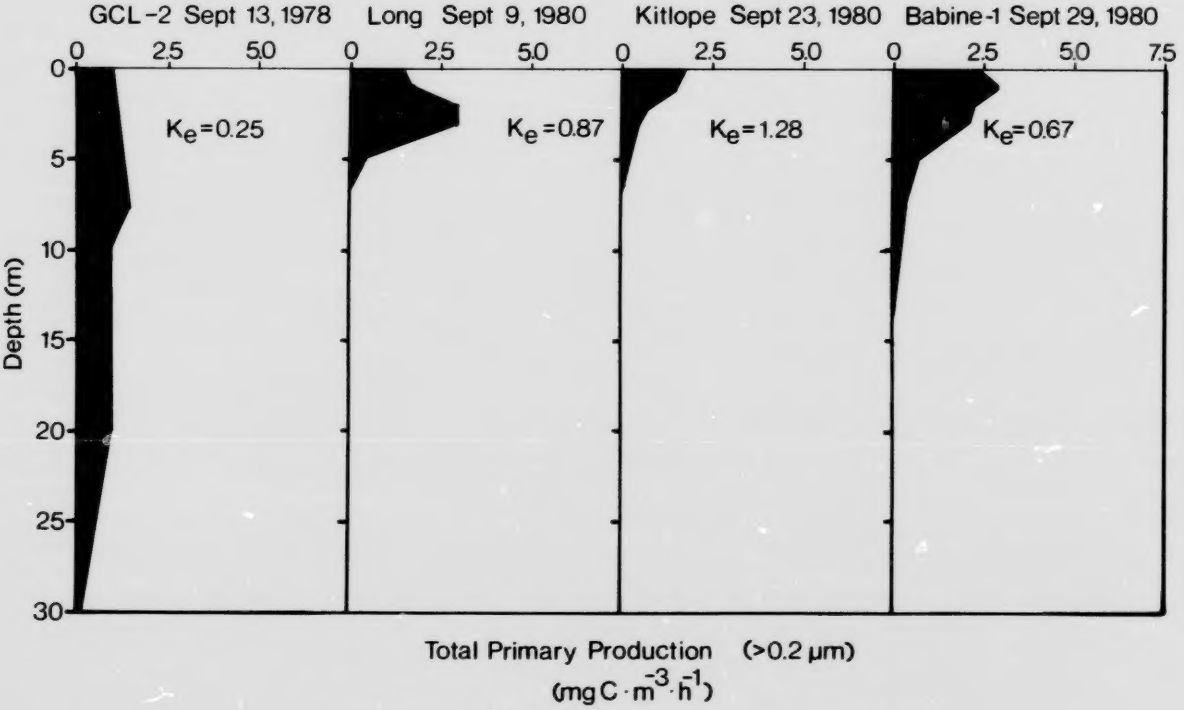


FIG. 3. Depth profiles of primary production in selected B.C. sockeye lakes.

Vertical profiles — Production profiles from humic coastal lakes (Long Lake) show some surface light inhibition, with shallow production peaks at depths of 3 to 4 m, and a sharp decline in productin below 4 m (Fig. 3). This type of profile was first described from eutrophic systems (Rodhe 1958), and was designated the Type I profile (Findenegg 1964). Large, clear, south coast systems (e.g. Great Central Lake — G.C.L.) show more uniform (orthograde) vertical profiles, often extending below 20 m (Type II profile, (Findenegg 1964)). Such profiles are characteristic of clear, oligotrophic north-temperate lakes. Glacial lakes, because of higher turbidity and reduced light penetration, have high light attenuation coefficients (k_e), shallow euphotic zones, and usually show peak production in surface layers (Fig. 3). The production profile for interior Babine Lake is intermediate between the Type I and II profiles, showing peaks in the near surface layers but higher production extending to greater depths than is usually seen in the Type I profile (Fig. 3). Babine Lake is a mildly humic lake and the profile from this lake, although used to depict a "typical" interior system, is not entirely representative. Most interior Fraser River sockeye lakes are not dystrophic and tend to have greater compensation depths than Babine (Stockner and Shortreed 1983). One would expect to see less pronounced surface peaks, with higher production extending to greater depths.

The distribution of plankton in the euphotic zone will influence feeding patterns of both vertically migrating juvenile sockeye and zooplankton. North coastal dystrophic lakes have a shallow euphotic zone and epilimnetic temperatures average only 15°C, and thus should permit juvenile sockeye access to food throughout the growing season. However, in clear, south coastal and interior lakes epilimnetic temperatures can often exceed 20°C in July and August, and restrict access by juvenile sockeye to resources in the epilimnion for part of the growing season (Narver 1970; Stockner et al. 1980). Glacial lakes are more weakly stratified, experience lower epilimnetic temperatures, and their juvenile sockeye show less pronounced vertical migration patterns (T. Gjernes, Pacific Biological Station, Nanaimo, B.C., personal communication).

Daily response — In oligotrophic coastal lakes there is a strong positive relationship between incident radiation and the hourly volumetric carbon production rate (Stockner et al. 1980; Stockner 1981) (Fig. 4). Peaks in production coincide with maximum daily radiation periods, generally occurring between 1200–1300 h on cloudless days (Fig. 4). This pattern is in marked contrast to the out of phase early morning peak production responses noted by Schindler and Fee (1974) in the fertilized ELA lakes of northwest Ontario that were related to short periods of dissolved inorganic carbon limitation at high midday light levels.

Fertilization response — Rates of primary production for 4 days following aerial fertilization were studied on three lakes with similar results obtained from each experiment (Stockner et al. 1980; Shortreed and Stockner 1981). Integral daily production increased the day following nutrient application, reached maximum values (2× initial value) on the second or third day, and returned to pre-fertilization levels by the fourth day (Fig. 5). In dystrophic Lowe Lake the production peak was consistently in the surface (0–1 m), in clear Great Central Lake it occurred at 2 m, and in Kitlope Lake at 5 m depth (Fig. 5).

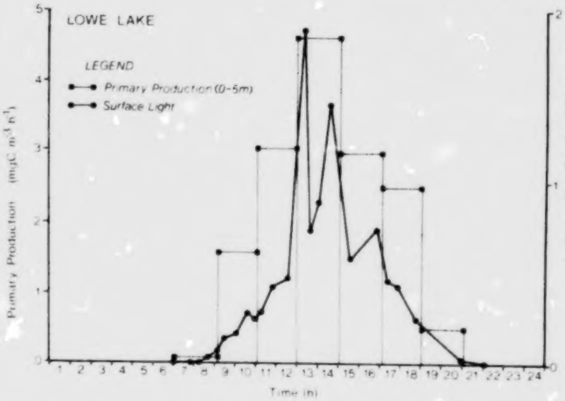
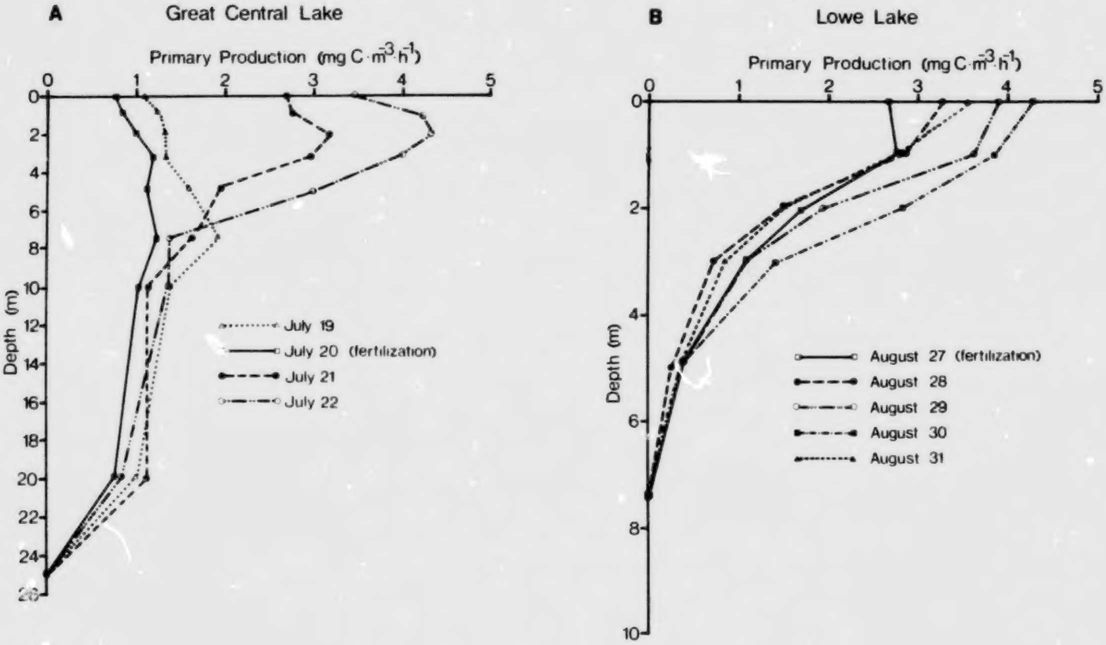


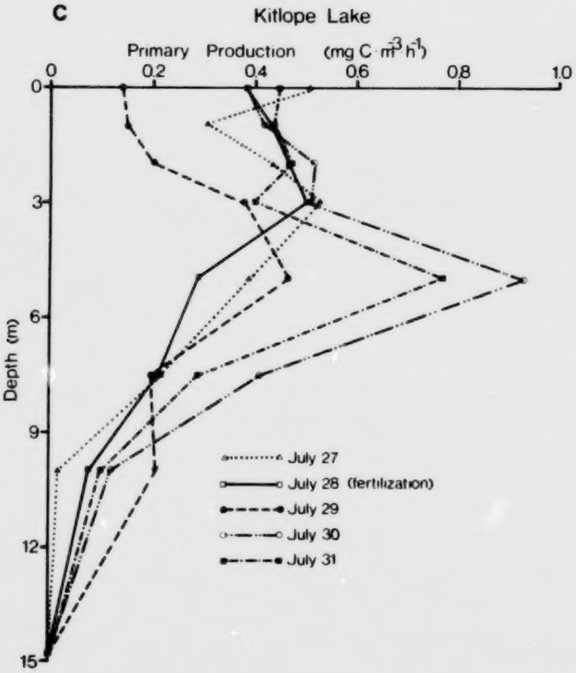
FIG. 4. Hourly primary production and light intensity relationship in Lowe Lake, August 29, 1979.

The amount of new carbon produced after each weekly fertilizer application was related to the phosphorus loading rate, which ranged from 3.5–7.5 mg P • m^{-2}• wk^{-1} in the experiments described. The carbon production rate measured on the third day after treatment was about double the rate measured on the day of fertilization (day 0) (Stockner et al. 1980; Shortreed and Stockner 1981). The weekly primary production increase was observed only in the fertilized zone of the lakes. During the Great Central Lake experiment, primary production was also monitored daily at a control station 6 km from the fertilized region, and no increase was observed in either carbon production or nutrient concentrations over the 4-day period of the experiment.

Size-fractionated production — In light of the ability of bacteria and small pico- (0.2–2 µm) and nanoplankton (3–20 µm) to exhibit high nutrient uptake and growth rates at low nutrient concentrations (Smith and Kalff 1982; Currie and Kalff 1984), their abundance and attendant contribution to carbon production in oligotrophic sockeye nursery lakes is not surprising (Costella et al. 1979; MacIsaac et al. 1981; Stockner 1981; Stockner and Shortreed 1983). In south coastal Kennedy Lake before treatment each size fraction contributed about equally to total production (Fig. 6). However, with treatment there was an increase in primary production and a shift to a proportionately much greater contribution by the picoplankton fraction. In fertilized north coastal dystrophic lakes (Curtis and Bonilla lakes) and in glacial lakes (Kitlope Lake), pico- and nanoplankton fractions are also major contributors to annual carbon production, but there is a higher contribution by microplankton in more humic systems, especially when they are subjected to high fertilizer loading rates (>10 mg P • m^{-2} • wk^{-1}) (Fig. 7 A–C).

July or August dates were selected from representative lakes to illustrate the size-fractionated production response with depth. The vertical profile from fertilized Kennedy–Clayoquot Arm showed picoplankton to be responsible for most carbon production at nearly all depths, but in unfer-





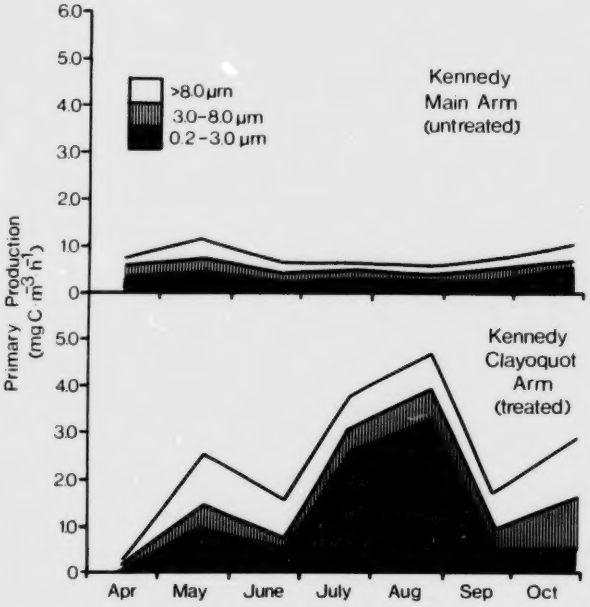


FIG. 5. Daily rates of primary production in coastal sockeye lakes following aerial application of fertilizer: A. Great Central, 1978. B. Lowe Lake, 1979. C. Kitlope Lake, 1980.

FIG. 6. Seasonal size-fractionated primary production in coastal Kennedy Lake, 1983 (Clayoquot Arm (treated), Main Arm (untreated)).

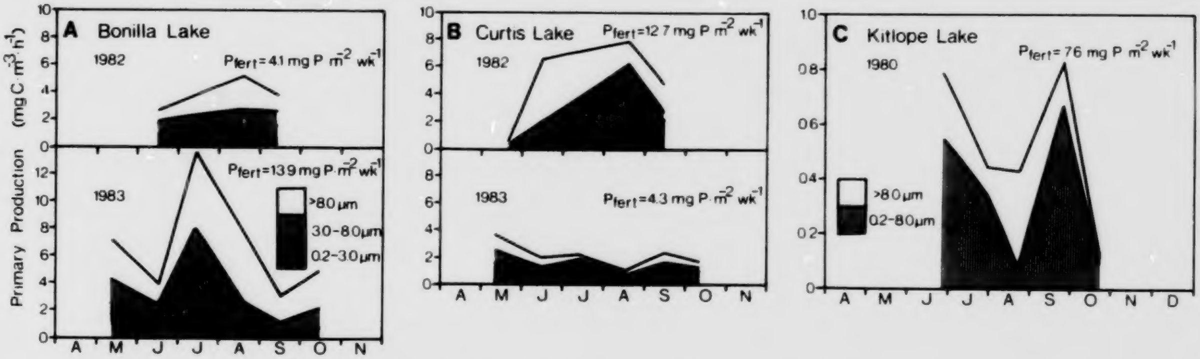


FIG. 7. Seasonal size-fractionated primary production in A. humic Bonilla Lake, (1982, 1983) and B. Curtis Lake (1982, 1983) under differing fertilizer P loading rates; and in C. glacial Kitlope Lake, 1980.

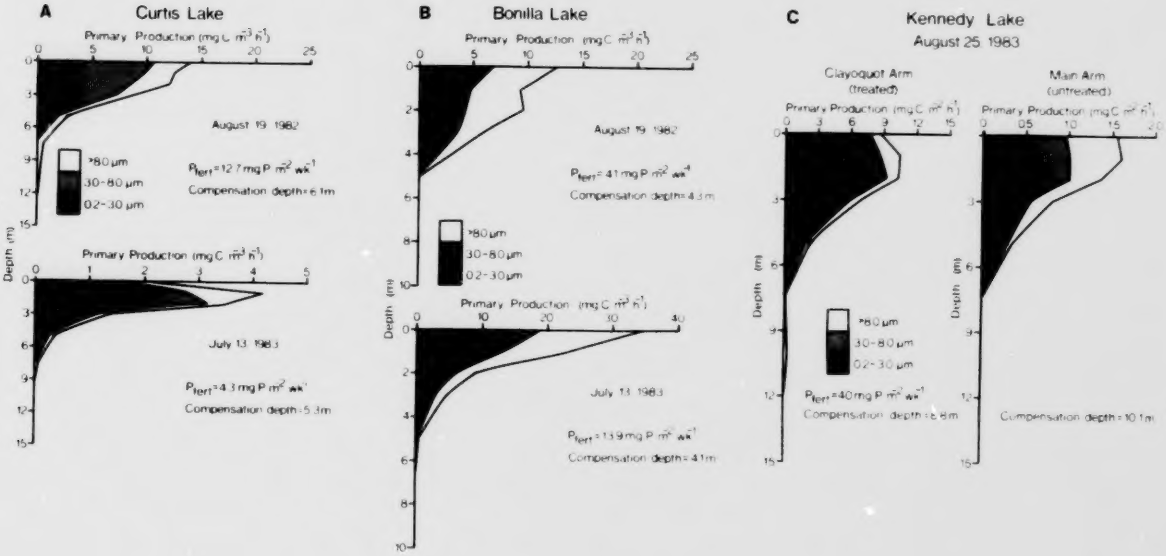


FIG. 8. Typical vertical profiles of size-fractionated primary production in A. coastal Kennedy Lake, B. & C. coastal humic Bonilla and Curtis lakes. (Note scale changes on production axis).

tilized Kennedy–Main Arm, where the daily rates are exceedingly low, production was divided more uniformly between the three size fractions (Fig. 8C). In dystrophic Curtis Lake, pico- and nanoplankton were major producers at most depths in 1983 under a low weekly phosphorus fertilization load, but under high loads in 1982 the nano- and microplankton portion (>3 µm) was responsible for up to 75% of the areal daily carbon production (Fig. 8A). In more humic Bonilla Lake, the vertical profile showed an even greater nano- and microplankton contribution to daily production (Fig. 8B). The shift to larger size classes at higher nutrient concentrations is similar to results obtained by others in both laboratory and field studies (Lehman and Sandgren 1982; Smith and Kalff 1982; Banse 1982).

The large contribution made by small algal picoplankton and nanoplankton to total carbon production in oligotrophic marine and freshwater ecosystems is now well documented (see review, Stockner and Antia 1986). Though size-fractionated primary production has not been studied on large, interior British Columbia sockeye lakes, algal picoplankton are present in moderate abundance and are likely to be of significance to the carbon production of these lakes as well (Stockner and Shortreed 1983).

During the weekly fertilization sequence, pico- and small nanoplankton (0.2–8 µm) are the first to show a carbon production increase on the day immediately following treatment. This increase is sustained after treatment and followed sequentially by larger nano- and microplankton production increases on day 3 (Costella et al. 1979; LEP unpublished data).

PHOSPHORUS BUDGETS

Input–output phosphorus budgets were calculated for Great Central Lake based on three scenarios (Table 3). Scenario 1 looks at the budget from 1958 to 1968 when the lake had a low average adult escapement (Manzer 1972) and was not fertilized. Scenario 2 depicts 1970–84 conditions with yearly nutrient addition and a higher adult escapement, whereas Scenario 3 presents a hypothetical budget for the lake, assuming maintenance of current escapement levels and termination of fertilization.

Fluvial inputs are the major source of phosphorus to the lake in all three scenarios, with phosphorus from adult carcasses contributing 7, 15, and 23% of the total P input (Table 3). Since the commencement of lake fertilization in 1970, the phosphorus from fertilizer to Great Central has averaged about 35% of the total input. Discharge represents the major output of phosphorus from the lake, with smolts representing only a very small fraction (1–5%) of total output.

TABLE 3. Mean annual phosphorus budgets for Great Central Lake under differing treatment and adult sockeye escapement scenarios.

Scenario:	1		2		3	
Escapement: Condition: Years:	Low[a] Unfertilized 1958–68		High[b] Fertilized 1970–84		High[b] Unfertilized 1972–84	
INPUT	kg P	%	kg P	%	kg P	%
Fluvial	5 482	85	5 482	46	5 482	71
Precipitation	496	8	496	4	496	6
Adult sockeye	448	7	1 787	15	1 787	23
Fertilizer	0	0	4 217	35	0	0
TOTAL	6 426	100	11 982	100	7 765	100
OUTPUT						
Sockeye smolts	23[c]	1	150[c]	5	91[d]	3
Discharge	1 547	99	2 884	95	1 868	97
TOTAL	1 570	100	3 034	100	1 960	100
Net P-input	4 856		8 948		5 805	
Retenton (%)	76		75		75	
P-smolts						
net P-input	0.5%		1.7%		1.6%	

Assumptions:

1. Mean annual discharge Stamp River (13 yr) at lake outlet, 1.69 km^3 yr^{-1}.
2. Mean epilimnetic TP concentration 1.7 mg P•m^{-3}
3. 4.24 kg P•T^{-1} (1000 kg) of smolt biomass, smolt biomass 35.4 T (14 yr. ave.).
4. 8.3 g P/fish in escapement.

[a] 54 000.

[b] 215 650.

[c] Egg–smolt survival, 4.0%; average smolt weight, 2.5 g.

[d] Egg–smolt survival, 2.5%; average smolt weight, 2.5 g.

The yearly retention (R) of phosphorus can be calculated using the formula (Dillon and Rigler 1974):

$$(1) \quad R_p = 1 - \frac{\text{P output}}{\text{P input}}$$

About 75% of the total phosphorus input is retained in Great Central Lake. A small fraction will remain as living biomass; a larger fraction will occur as dissolved phosphorus; but the majority will be bound in the deep-water sediments. The well-oxygenated surficial sediments of deep, oligotrophic lakes such as Great Central will effectively sequester this phosphorus with no net release to the water column (Bostrom et al. 1982). Sediment loss was not calculated for Great Central Lake, but can be as high as 50–60% of the annual P input in warm, monomictic coastal lakes (Edmondson and Lehman 1981).

Only a very small proportion (0.5%) of the net P-input is retained by juvenile sockeye populations in Great Central Lake in years of low escapement and no treatment; however, in years with fertilization and high escapement the ratio shows a threefold increase (1.7%), suggesting more efficient trophic transfer to juvenile sockeye populations. Without treatment but with maintenance of high escapement (Scenario 3) a similar amount of phosphorus (1.6%) passes to sockeye smolts as in the fertilized conditions, but fewer smolts of smaller size are produced.

It was informative to compare the phosphorus budget for Great Central Lake with other sockeye nursery lakes on the Pacific coast of North America (Washington, Babine, Iliamna) and on the Kamchatka Peninsula, USSR (Lake Dalnee) (Table 4). Fluvial inputs were the most important source of phosphorus in all lakes except Iliamna on the peak cycle years. Phosphorus input from returning adults ranged from as little as 3% of the total in Lake Washington to as much as 58% in Iliamna. Discharge was the largest phosphorus output with outmigrant smolts representing only from 1 to 20% of the total, except in Iliamna in 1964, when smolts from a peak cycle brood accounted for 41.6% of the output (Table 4). Apparently smolt migration can represent a significant fraction of P removal on certain years in large lakes where stocks exhibit strong cyclic dominance. Values of phosphorus retention (R) were similar in all lakes, averaging 50–75%, except in Lake Dalnee (20%), which has a high discharge rate and an extremely short water residence time (Krokhin 1957).

Some lakes (Babine, Dalnee, Iliamna) appear to make more effective use of a given annual P-load than others (Great Central, Washington), as shown by values of the ratio P-smolts: net P-input. This is because some lakes exhibit an extreme oligotrophic (food-limited) condition (Great Central Lake) or have small juvenile sockeye populations which make little impact on available food resources (Lake Washington). Alternatively, a small P-smolt: net P-input ratio might also result if large portions of P-input are unavailable for autotrophic production (e.g. winter input-flushing, glacial sediment).

To better compare the contribution of phosphorus from adult salmon carcasses with that from fertilizer applications one must better understand both the spatial and temporal effects of these inputs on pelagic communities. I have chosen Bonilla Lake, a small fast-flushing north coastal nursery lake, to illustrate temporal changes in the P budget during the

TABLE 4. Annual phosphorus budgets for selected sockeye salmon nursery lakes.

Lake:	Great Central		Babine[1]		Washington[2]		Dalnee[3]		Iliamna (1964)[4]		Iliamna (1965)[4]	
INPUT	kg P	%	kg P	%	kg P	%	kg P	%	kg P	%	kg P	%
Fluvial	5 482	46	18 252	66	53 000	83	800	70	105 000	87	115 000	39
Precipitation	496	4	1 392	6	8 680	14	75	7	8 000	7	8 000	3
Adult sockeye	1 787[a]	15	7 806[b]	28	1 907[c]	3	260[d]	23	7 000	6	169 000	58
Fertilizer	4 217	35	0	0	0	0	0	0	0	0	0	0
TOTAL	11 982	100	27 450	100	63 487	100	1 135	100	120 000	100	292 000	100
OUTPUT												
Sockeye smolts	150[a]	5	1 896[b]	20	201[c]	1	20[d]	2	25 000[c]	42	10 000[e]	13
Discharge	2 884	35	7 428	80	24 050	99	890	98	35 000	58	69 000	87
TOTAL	3 034	100	9 324	100	24 251	100	910	100	60 000	100	79 000	100
Net P-input	8 948		18 126		37 630		225		60 000		213 000	
Retention (%)	75		66		61		20		50		73	
P-smolts												
Net P-input	1.7%		10.4%		0.5%		8.1%		41.6%		4.7%	

[a] Average 1970–84, G. Steer (personal communication).
[b] Average 1973–85, H. D. Smith (personal communication).
[c] Average 1974–84, J. Ames (personal communication).
[d] Average 1937–47.
[e] 1965, peak cycle year.

[1] Stockner and Shortreed (1974).
[2] Edmondson and Lehman (1981).
[3] Krokhin (1959).
[4] Donaldson (1966).

growing season (Table 5). From April to October, fertilizer P input to the epilimnion contributed 90% of the total input, compared with only 7% from fluvial sources. Returning adults contributed only 2% to total input. The greatest outputs during the growing season were by discharge, with outmigrant sockeye smolts removing less than 1% of the total P input from the lake. Phosphorus retention during the growing season was 63%, the majority of which passed to the zooplankton in the pelagic community (Table 5). Forty-two percent of the retained phosphorus was lost to the sediment during the growing season.

The Bonilla Lake budget illustrates the importance of phosphorus from fertilizer to P budgets of treated coastal lakes, and explains why Stockner and Shortreed (1985) found such highly significant correlations between fertilizer load ($\text{mg P} \bullet \text{m}^{-2} \bullet \text{wk}^{-1}$) and TP, chlorophyll, and primary production in British Columbia coastal lakes. It also demonstrates that nutrient input from adult salmon carcasses is likely to be of far less significance in the nutrient dynamics of coastal monomictic lakes than in interior dimictic lakes, mainly because of the increased probability of nutrient loss by winter flushing in coastal lakes. The hydrologic cycle of dimictic lakes should theoretically permit higher nutrient retention and concomitant higher nutrient concentrations. To illustrate these points I have constructed an idealized temporal P budget for treated and untreated coastal (warm monomictic) and interior (dimictic) B.C. sockeye lakes (Fig. 9). The surface application of fertilizer to the epilimnion directly targets the plankton community and can rapidly lead to increased primary and secondary production (LeBrasseur et al. 1978; Stockner and Hyatt 1984). By contrast, phosphorus release from adult carcass decomposition in autumn can be a protracted and inefficient energetic process, with entry into littoral, zoobenthic, heterotrophic, and/or detrital pathways prior to incorporation into plankton and the intended juvenile sockeye salmon target (Mathisen 1966; Donaldson 1966; Krokhin 1957; Sorokin and Paveljava 1978). This suggests that phosphorus from adult carcasses will be a more effective contributor to the phosphorus budgets of interior dimictic lakes than in coastal monomictic lakes. It also suggests that adult escapements must be high enough to significantly contribute to the net phosphorus input to lakes and that escapements must be maintained at reasonable levels over several seasonal cycles to be effective.

PHYTOPLANKTON SIZE SPECTRA

Sockeye are obligate planktivores which tend to select larger zooplankton (> 1.0 mm) if they are available (Krokhin 1959; Johnson 1965; Narver 1970; Goodlad et al. 1974; Northcote et al. 1978). As a result, zooplankton communities of many coastal sockeye lakes are dominated by small herbivorous and predaceous zooplankton (e.g. rotifers, *Bosmina, Cyclops*) at very low population densities (LeBrasseur and

TABLE 5. Phosphorus budget for Bonilla Lake, April to October, 1980.

INPUT (April–October)	kg P	%			
Fluvial	47	7			
Precipitation	7	1			
Adult Sockeye	16	2			
Fertilizer	619	90			
TOTAL	690	100			
OUTPUT (April–October)					
Sockeye smolts	3	1			
Discharge	252	99			
TOTAL	255	100			
Net P-input	435				
Retention (%)	63				
Pelagic Community			April kg P	October kg P	Net Change kg P
Phytoplankton + dissolved P			93	147	+54
Zooplankton			8	204	+196
Fish			1	5	+4
TOTAL			102	356	+254
Sediments			—	—	181

Assumptions:

1. August P concentration in rainfall plus runoff (2 µg/L).
2. 1980 adult escapement 2 141 at 1.75 kg/fish and 0.365% P/wt. weight (assumed decomposed and distributed throughout the water column by October).
3. 1980 pre-smolts 115 000 at 3.66 g/fish and 0.432% P by weight.
4. 1980 sticklebacks 528 000 at 1.6 g/fish.
5. zooplankton AFDW (ash-free dry weight) × 1.08 = total organic weight (TOW) and 2.1% of TOW = P.
6. flushing = runoff; discharge during growing season is only epilimnetic water (shallow outlet).

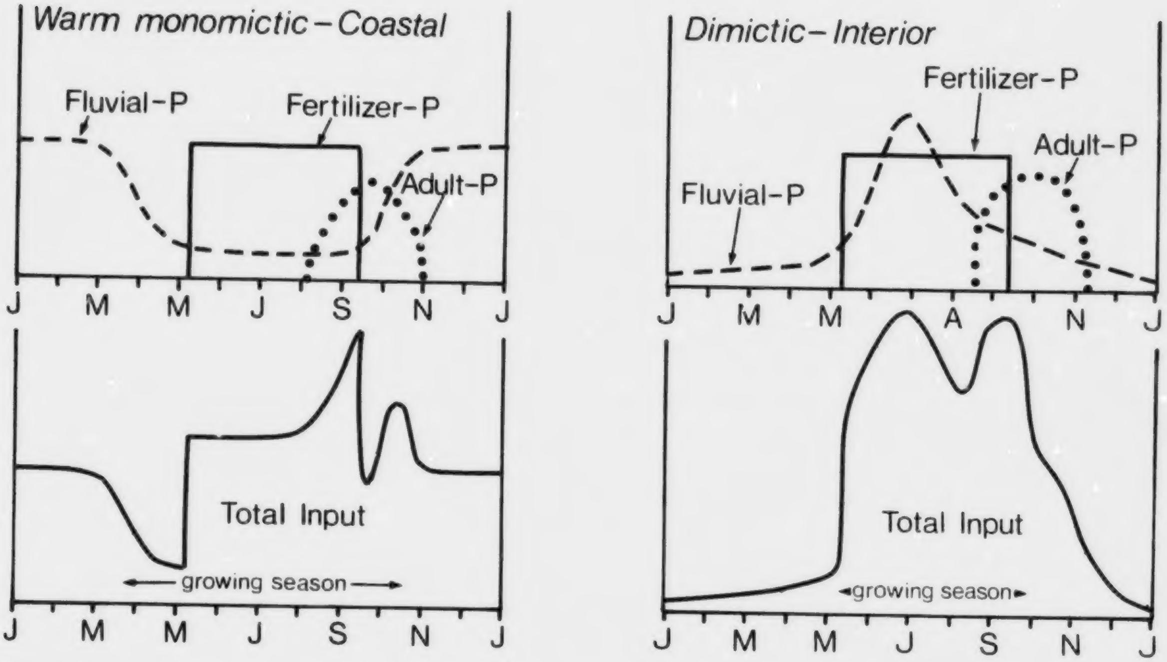


FIG. 9. Temporal sequence of major phosphorus inputs to fertilized coastal monomictic and interior dimictic sockeye nursery lakes.

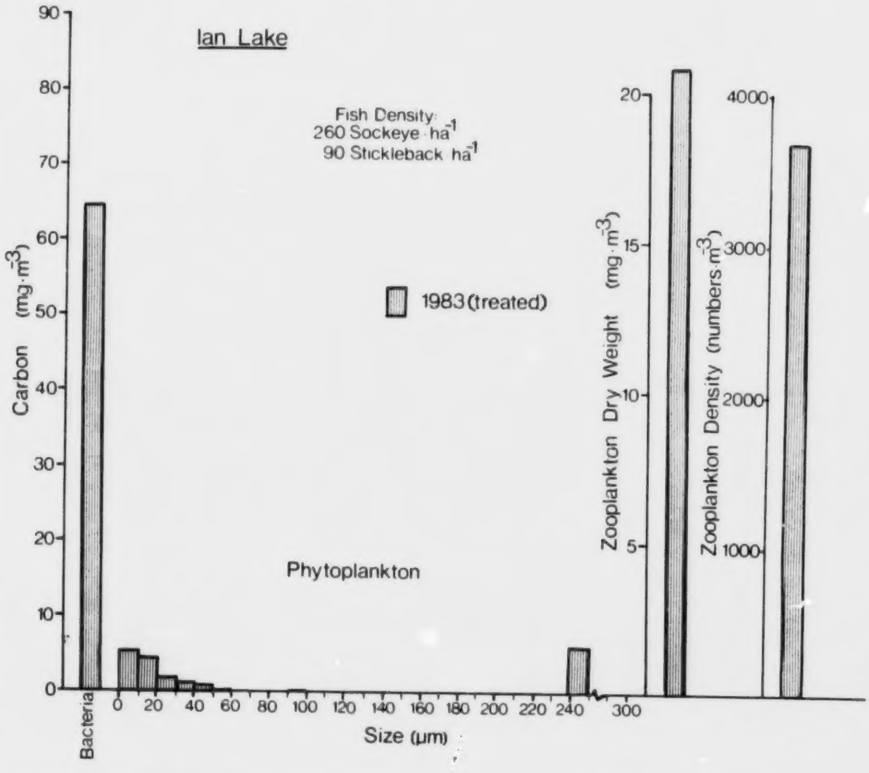


FIG. 10. Phytoplankton community size frequency spectra and zooplankton biomass and numbers for Ian Lake, Sept. 13, 1983.

Kennedy 1972; Rankin et al. 1979; Rankin and Ashton 1980). These small crustacean zooplankton, together with microzooplankton (<0.2 mm) (protozoans, rotifers, nauplii) generally utilize only pico- and nanoplankton within the size range 0.2–15 µm (Gliwicz 1975; McCauley and Downing 1985). The general paucity of large herbivorous zooplankton (e.g. *Daphnia,*) in coastal sockeye lakes should theoretically permit the accumulation of larger microphytoplankton (>20 µm) (Lynch 1979; Lynch and Shapiro 1981; Spencer and King 1984; Infante and Litt 1985).

Phytoplankton size spectra were examined from August or September dates from three coastal lakes with varying zooplankton and pelagic fish densities and both treated and untreated conditions. In treated Ian Lake, with lowest fish and highest zooplankton densities, phytoplankton biomass was very low and the size frequency spectra relatively flat, and slightly skewed toward smaller cells, with bacteria the dominant size fraction (Fig. 10).

Yakoun Lake (untreated) had less zooplankton biomass and higher fish densities (2000 fish/ha) than Ian Lake, and had a greater accumulation of both small (0–40 µm) and larger phytoplankton (>90 µm) than Ian Lake (Fig. 11). Yakoun (treated) had greater quantities of both fish and zooplankton than in the untreated year, yet phytoplankton showed a similar shaped size-frequency spectra. Fertilization did not alter phytoplankton quality (size), only quantity, at least on the dates of comparison (September 5 and 13 for Yakoun and Ian lakes, respectively). As in Ian Lake the highest carbon biomass was in the bacteria fraction.

In Kennedy Lake, both treated Clayoquot Arm and untreated Main Arm had higher fish densities than either Ian or Yakoun lakes. The profiles from Yakoun (untreated) and Main Arm, Kennedy Lake (untreated) with similar fish and zooplankton densities were nearly identical; however, in fertilized Clayoquot Arm, where the greatest fish density and lowest zooplankton biomass occurred, there were higher numbers of pico-, nano-, and microplankton (Fig. 12). Bacterial biomass was lower in Kennedy Lake than in Ian or Yakoun lakes, which may reflect higher abundances and grazing by flagellates and microzooplankton.

FOOD-CHAIN LINKS AND SINKS

The weekly application of fertilizer to coastal sockeye lakes has resulted in substantial increases in the production rate and biomass of bacteria and of pico- and small nanoplankton in the 0.2–8 µm size range (Costella et al. 1979; Stockner et al. 1980; MacIsaac et al. 1981). Rotifers have also shown marked increases in both biomass and numbers of species (LeBrasseur and Kennedy 1972; Rankin et al. 1979; Rankin and Ashton 1980); and this increase in fertilized lakes can be linked directly to large increases in their food resources (particles <15 µm) (Allan 1976; Richman et al. 1985) and to their immunity from serious vertebrate predation and selective predation by fish on their invertebrate predators (copepods) (O'Neill and Hyatt 1987). It is likely that in untreated coastal lakes with low densities of pico- and nanoplankton, rotifer populations are severely food-limited,

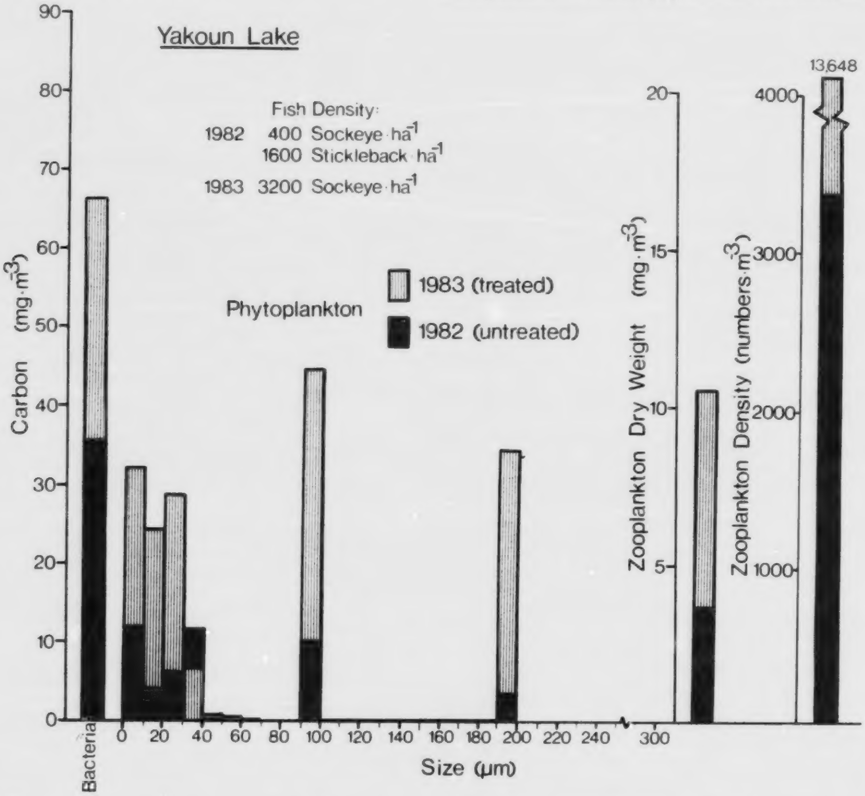


FIG. 11. Phytoplankton community size frequency spectra and zooplankton biomass and numbers for Yakoun Lake, Sept. 5, 1982; Sept. 13, 1983.)

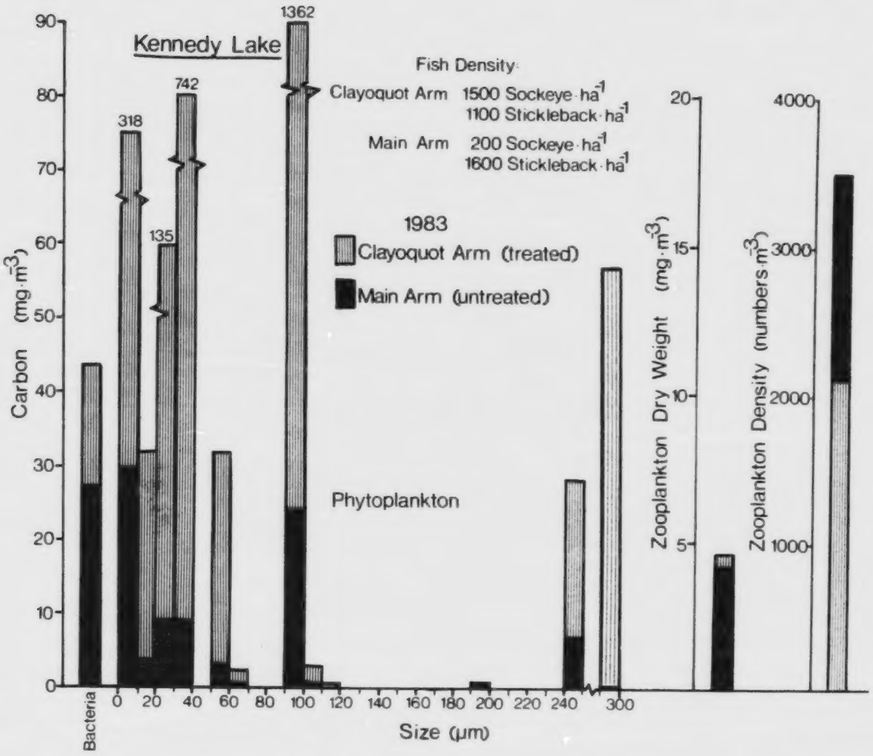


FIG. 12. Phytoplankton community size frequency spectra and zooplankton biomass and numbers for Kennedy Lake, Clayoquot and Main Arms, August 25, 1983.)

rarely attaining growth rates close to their maximum (Banse 1982; Starkweather et al. 1979; Stemberger and Gilbert 1985). Rotifer increases in fertilized lakes may also be linked to increases in micro-heterotrophic flagellates and ciliates that are also well within their preferred food size-range (1–15 µm). When crustaceans and rotifers were temporarily eliminated by rotenone from a small Swedish lake, and grazing pressure eliminated, ciliates increased in density and expanded their range (Stensen 1985). Selective removal in the laboratory of rotifers and larger zooplankton from coastal Hobiton Lake water using 54 µm screens, resulted in rapid depletion of picoplankton and dominance by micro-heterotrophic flagellates (E. MacIsaac, West Vancouver Laboratory, West Vancouver, B.C., personal communication).

Juvenile sockeye feeding on large herbivorous zooplankton (*Daphnia*, *Diaptomus*) are but 2 steps removed from the autotrophic food base, and transfer of energy from phytoplankton to fish is more direct and efficient. Conversely, sockeye forced by the scarcity or absence of larger zooplankton to feed primarily on copepods or other small bodied zooplankton may potentially be 4 steps removed from the food base, and since energy losses are from 50 to 90% at each step in the food chain, transfer of energy from phytoplankton to sockeye tends to be diffuse and inefficient. I have depicted several of the more important possible pathways of energy transfer in Pacific coastal and interior B.C. lakes to illustrate the point that sockeye can potentially feed at several trophic levels in nursery lakes (Fig. 13). I believe that one of the reasons sockeye smolts leaving coastal and glacial lakes are, on average, much smaller than from interior systems is related to the extreme oligotrophic condition of coastal and glacial lakes, which structures their food-webs and causes diminished trophic efficiency. In these ultraoligotrophic systems sockeye fry must expend more energy to capture the smaller *Bosmina* and evasive copepods and rotifers. Clearly, more food-web research is required, however, observations on juvenile sockeye diet in coastal and interior lakes tend to be supportive of the "trophic level" hypothesis.

Most interior sockeye lakes have a far greater abundance of larger zooplankton (>1.0 mm) than coastal lakes, e.g. *Daphnia*, *Bosmina*, *Diaptomus*, *Heterocope*, and analysis of juvenile sockeye stomach contents verifies that they are often dominant prey items (Johnson 1965; Narver 1970; Rankin 1977; Goodlad et al. 1974; I. Williams and K. Morton, Cultus Lake Laboratory, Cultus Lake, B. C., personal communication). Large bodied zooplankton can also occur in some coastal lakes where pelagic fish densities are exceedingly low (e.g. Ian and Awun lakes on the Queen Charlotte Islands), but generally they are uncommon and, when present, occur at very low population densities. Common prey items of juvenile sockeye and pelagic sticklebacks in coastal lakes are typically the raptorial copepod *Cyclops*, the omnivore *Epischura*, and the smaller bodied forms of *Bosmina* (Barraclough and Robinson 1971, 1972; P. Rankin, Pacific

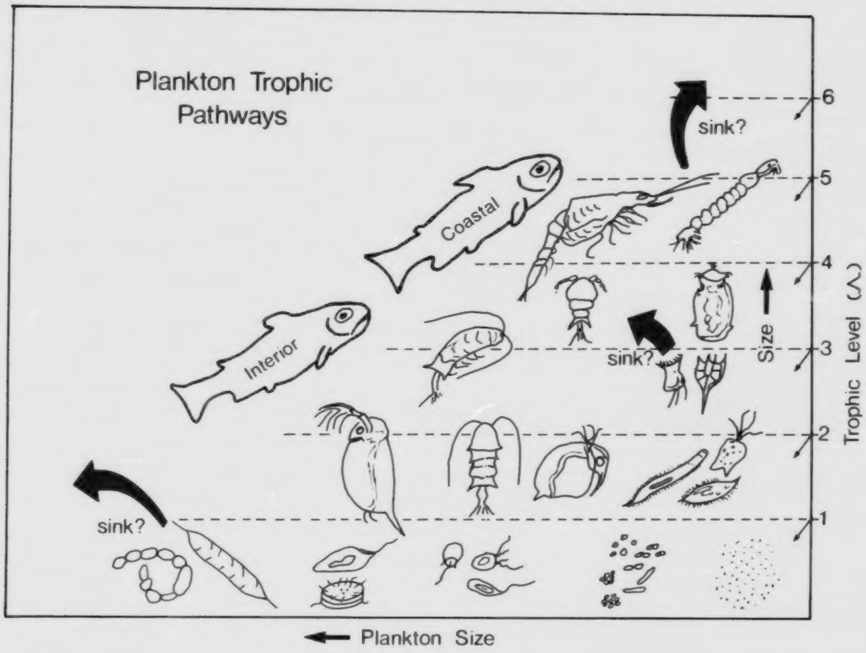


FIG. 13. Potential trophic pathways in pelagic communities of sockeye lakes plotted in relation to size and trophic level.

Biological Station, Nanaimo, B.C., personal communication). Though *Daphnia* populations increased following the first fertilization of Great Central Lake in 1970, they declined rapidly in subsequent years, and since 1977 have been uncommon (Rankin et al. 1979). It is likely that the scarcity of *Daphnia*, and other large zooplankton, is due to their inability to maintain reproductively viable populations in such oligotrophic lakes when subjected to size-selective predation pressure from pelagic fish populations. It is likely that even in fertilized lakes with greater food availability their population loss rates would still exceed reproductive rates (Hall et al. 1976; Lynch 1979). The ubiquity of *Daphnia* in interior sockeye lakes must be related to the higher rates of primary productivity in these lakes, but also may be due to the common quadrennial cyclic dominance of many sockeye populations which can relax grazing pressure on *Daphnia* populations between peak cycle years.

Although biologically mediated control of pelagic zooplankton communities is most often used to explain species composition, size distribution, and productivity (Peters 1983; Sprules et al. 1983; Carpenter and Kitchell 1984; Bergquist et al. 1985), some authors have shown that climatic and other abiotic influences are of greater importance in structuring zooplankton communities (Sorokin and Paveljeva 1978; Cushing 1982; George and Harris 1985; Koenings et al. 1986). The matching or mismatching of food resources at critical periods of the year, notably the timing and duration of the spring bloom, is central to arguments of climatic or abiotic control. In Lake Windermere, spring epilimnetic temperatures, rather than planktivorous fish grazing, seem to determine the composition and abundance of zooplankton populations (George and Harris 1985). In Lake Dalnee during a typical warm year (1970), microbial communities are much more productive and heterotrophic microzooplankton (protozoans, rotifers, nauphlii) can utilize up to 70% of the phytoplankton production creating a less trophically efficient system for sockeye (Sorokin and Paveljeva 1981). Lake Dalnee in 1971 was cooler, microbial activity was less, and heterotrophic microplankton utilized only 25% of phytoplankton production. The remainder was grazed by large zooplankton, *Daphnia* and *Diaptomus*, and the simpler, shorter food-chains resulted in higher trophic efficiency. In Alaskan glacial lakes, particle turbidity interferes with the filter feeding cladocerans *Bosmina* and *Daphnia* and they are totally absent from these lakes (Koenings et al. 1986). Clearly both biotic and abiotic processes can influence zooplankton community structure and production. Perhaps climate sets the initial direction of succession with predator-prey interactions determining the final product (community structure).

The potential length of the energy pathway (transfer steps) from phytoplankton carbon to sockeye biomass can be considered a constraint on the seasonal growth of sockeye in lakes. Whether or not the longer picoplankton->protozoan->microzooplankton->zooplankton->sockeye food chain of oligotrophic coastal lakes should be considered a link or sink requires further research. Predation of rotifers by young limnetic sticklebacks, and of *Bosmina* and *Cyclops* by adult sticklebacks can be considered a sink in coastal sockeye lakes because the competitive interaction with sockeye for zooplankton can reduce sockeye growth and survival (O'Neill and Hyatt 1987). The invertebrate predators *Neomysis* and *Chaoborus* can also be effective competitors with sockeye for zooplankton in some coastal lakes (Northcote et al. 1978).

Large phytoplankton (*Anabaena, Oscillatoria, Rhizosolenia, Peridinium*) are underutilized by zooplankton (Infante and Litt 1985; Gliwicz 1975) and when they occur can represent an energy sink, especially in interior dimictic sockeye lakes. Without careful control over fertilizer loading rates, N to P ratios and length of application period, large inedible microphytoplankton (20–200 µm) can rapidly increase and their accumulated biomass can represent a significant loss of nutrients and energy (Stockner and Hyatt 1984).

PREDICTION OF SMOLT YIELD

Many investigators have attempted, some with good success, to predict fish yield or biomass from primary productivity values or some estimate of phytoplankton biomass (carbon, total chlorophyll, total phosphorus) (Hrbacek 1969; Melack 1976; Oglesby 1977; Matuszek 1978; Hanson and Leggett 1982). The underlying premise is that base levels of autotrophic production in lakes should be causally related, via various trophic pathways, to fish biomass and production, and ultimately to the annual fish yield or harvest (Sheldon et al. 1982). In the majority of British Columbia coastal lakes, pelagic sticklebacks and juvenile sockeye are the dominant species, since resident or anadromous populations of trout or char, when present, occur at extremely low densities (Simpson et al. 1981).

Using data from 18 north temperate lakes, Hanson and Leggett (1982) showed a strong relationship between average lake total phosphorus concentrations and total fish biomass. Fish biomass estimates (derived from smolt weight and density) from several coastal lakes and Babine Lake lie close to Hanson and Leggett's (1982) regression line (Fig. 14). Though our values underestimate the total fish standing stock, they do illustrate the point that low fish biomass is a characteristic feature of oligotrophic B.C. lakes (Northcote and Larkin 1956; Stockner and Shortreed 1985).

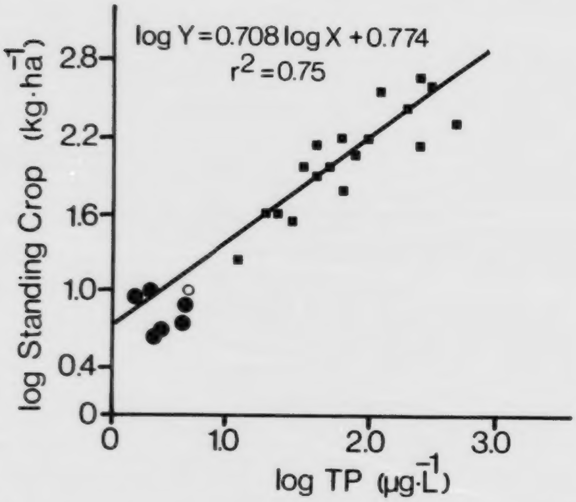


FIG. 14. Relationship between average total phosphorus (TP) and fish standing crop (■) North temperate lakes (Hanson and Leggett (1982) (○) Babine Lake, ave. 1973–85, (●) Coastal lakes (Great Central, Kennedy, Nimpkish).

Hyatt and Stockner (1985) have shown that on average a 69% increase in weight can be achieved when coastal lakes are fertilized, which suggests that either autotrophic production or an estimate of phytoplankton biomass, (TP, Chl) could be used to predict potential "yield" or mean smolt weight. Several variables were tested in univariate and multivariate analyses, but no significant correlations were obtained. Perhaps as more information from lakes showing wider ranges of fish densities and smolt weights becomes available, some meaningful empirical relationships will be established.

Summary and Conclusions

Lake fertilization has increased juvenile sockeye production and adult returns in some coastal lakes (LeBrasseur et al. 1978; Hyatt and Stockner 1985). Since fertilization response is site specific and dependent upon each lake's community structure and incipient nutrient levels, no single process can be identified as being responsible for the success of lake treatment. Its efficacy as a sockeye enhancement technique will also be dependent on pelagic fish densities (Hyatt and Stockner 1985), and on the presence or absence of their potential competitors. Some lakes with simple community structure will respond rapidly to fertilization, while others will create sinks and dissipate energy in inefficient pathways. Glacial lakes appear to be constrained by physical factors (turbidity, thermal instability) that lower temperature and primary production and create an ultraoligotrophic condition.

We believe that the reason we see favorable sockeye growth and survival in fertilized coastal lakes is related principally to increased primary production without significant alteration of plankton community structure and with maintenance of the oligotrophic condition. At the low fertilization loading rates (3–5 mg P • m^{-2} • wk^{-1}) and short application periods (ave. 18–20 wk) currently used on coastal lakes we have not increased average zooplankton biomass in fertilized lakes to levels even close to values for interior lakes (Johnson 1965; Rankin 1977; Goodlad et al. 1974; Stockner and Shortreed 1983). Further food-web process research and whole-lake fertilization experiments are required on coastal lakes to determine whether changes in fertilization strategies can stimulate coastal systems to mimic interior systems with respect to trophic efficiency and fish production.

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Population Characteristics of Sockeye Salmon (*Oncorhynchus nerka*) Smolts Relative to Temperature Regimes, Euphotic Volume, Fry Density, and Forage Base Within Alaskan Lakes

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Abstract

KOENINGS, J. P., AND R. D. BURKETT. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes, p. 216–234. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

An empirical classification of sockeye salmon (*Oncorhynchus nerka*) smolt production is based upon the population characteristics of density, freshwater age, and mean size (length and weight). Recruitment limited lake systems produced large (>60–65 mm; >2.0 g), and essentially all ($>85\%$) age 1. smolts. Smolts from rearing-limited lake systems were either all age 1. and of minimal or threshold mean size (60 mm, 2 g), or older and larger as a result of extended freshwater rearing. Verification of smolt population responses to changes in the fry/forage base ratio (intraspecific competition) was achieved by stocking one lake with increased densities of fry in successive years; and by annual fertilizer additions to the epilimnion of another. Smolt population characteristics proved to be very pliant, and exhibited a range of responses to increased fry density and lake fertility. In other lakes, juveniles had equivalent growth and the same smolt characteristics under lowered temperature regimes as under high fry densities; however, smolt population characteristics proved to be unresponsive to changes in either fry density or lake fertility. Threshold-sized smolts indicate a size limiting rearing environment which can be equally caused by abiotic (density independent) and biotic (density dependent) factors. Rearing limited smolt production (numbers and biomass) was highly ($P<0.005$; t-test) correlated to an index of areal rates of photosynthesis, — euphotic volume (EV), over a wide size range of oligotrophic lakes. A similar strong correlation was observed between adult sockeye production and euphotic volume. Thus, forecasts of smolt yield (23 000 smolts•EV^{-1}) and adult production (2 500 adult•EV^{-1}) can apply to a wide variety of sockeye nursery lakes. In additon, the ocean survival of smolts from particular regions must also be considered, since larger numbers of adults can return from smolt populations consisting of either: (1) less numerous but larger smolts, produced under density-dependent rearing, or (2) more numerous but smaller sized smolts, produced under density-independent rearing.

Résumé

KOENINGS, J. P., AND R. D. BURKETT. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes, p. 216–234. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Une classification empirique de la production de smolts de saumon nerka (*Oncorhynchus nerka*) est faite à partir des caractéristiques de la population aux points de vue de la densité, de l'âge en eau douce et de la taille moyenne (longueur et poids). Les systèmes lacustres à recrutement limité ont produit de gros smolts (>60–65 mm; >2.0 g), qui étaient pratiquement tous (>85 %) d'âge 1.. Les smolts provenant de systèmes lacustres à croissance limitée étaient soit tous d'âge 1. et avaient une taille moyenne minimale ou de palier (60 mm; 2 g), ou étaient des individus plus âgés et plus gros par suite d'une période d'élevage prolongée en eaux douces. La vérification des réactions des populations de smolts aux changements dans le rapport de base alevins/poissons fourrage (compétition intraspécifique) a été réalisée en repeuplant un

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lac avec des densités accrues d'alevins au cours d'années consécutives et en ajoutant à chaque année un fertilisant à l'épilimnion d'un autre lac. Les caractéristiques de la population de smolts se sont avérées très flexibles et les réactions ont été variées face à une densité accrue d'alevins et à une fertilité plus grande du lac. Dans d'autres lacs, les jeunes avaient une croissance équivalente et les mêmes caractéristiques de smolts à des régimes de températures plus basses que lorsque la densité des alevins était élevée; cependant, les caractéristiques de la population de smolts se sont avérées insensibles aux changements dans la densité des alevins ou dans la fertilité du lac. Les smolts de taille de palier indiquent un milieu d'élevage limitant la taille qui peut être tout aussi bien causé par des facteurs abiotiques (indépendants de la densité) que par des facteurs biotiques (dépendants de la densité). On a établi une forte corrélation ($P<0.005$; test de *t*) entre la production (quantités et biomasse) de smolts de croissance limitée et un indice des taux de photosynthèse par unité de surface, le volume euphotique (VE), sur une vaste gamme de tailles des lacs oligotrophes. On a observé une forte corrélation semblable entre la production de saumon nerka adulte et le volume euphotique. Par conséquent, les prévisions de la production de smolts (23 000 smolts•VE^{-1}) et de la production d'adultes (2 500 adultes•VE^{-1}) peuvent s'appliquer à une grande variété de lacs servant à la croissance des saumons nerkas. En outre, on doit également tenir compte de la survie en mer des smolts provenant de certaines régions, étant donné que de grandes quantités d'adultes peuvent remonter à partir de populations de smolts constituées soit : 1) de smolts moins nombreux mais plus gros, produits dans des conditions d'élevage dépendant de la densité ou 2) de smolts plus nombreux mais de taille plus petite, produits dans des conditions d'élevage indépendantes de la densité.

Introduction

Primary concerns in the management of sockeye salmon (*Oncorhynchus nerka*) are the influence of changing climate (George and Harris 1985), fishing presure (Larkin 1977), habitat alteration (Hrbacek 1969; Lloyd et al. 1987), and other forms of stress (Rigler 1982). Yet, the current cornerstone of sockeye management is successful juvenile recruitment arrived at through manipulations of the escapement. The assumption is that stock size can be controlled merely by increasing or decreasing numbers of spawners (Ricker 1954; Rounsefell 1958; Larkin 1977). However, Juday et al. (1932), Ricker (1937), Ruggles (1965), Mathisen (1972), Goodlad et al. (1974), and Hyatt and Stockner (1985) have argued that this defines the system too narrowly and that physical and chemical variables as well as other organisms in the freshwater nursery area must be considered. In fact, Mathisen (1972) concluded that spawner–recruit relationships must be based on parameters which take into account changes in lake productivity. One reason is that adult carcasses can contribute significant amounts of nitrogen and phosphorus to nursery lakes (Juday et al. 1932; Barnaby 1944; Nelson 1958; Krokhin 1967; Mathisen 1972; Richey et al. 1975; Koenings et al. 1985) which may stimulate primary production (Donaldson 1967; Gadau 1966).

The factor driving, and some times limiting, aquatic productivity in north temperate oligotrophic sockeye lakes is the nutrient supply entering the euphotic zone (Nelson 1958; Hyatt and Stockner 1985). Moreover, there appears to be a definite food chain linkage between increased nutrient loading (Hanson and Leggett 1982), primary production (Hrbacek 1969; Melack 1976; McConnell et al. 1977; Liang et al. 1981), secondary production (Dermott et al. 1979), and increased fish yield. Specific to sockeye salmon, Nelson (1958) quite clearly showed a positive correlation between growth in four age classes of sockeye smolts, and increases in photosynthesis in Bare Lake, Alaska.

Successful sockeye fry rearing also requires that production of preferred forage items is timed to coincide with the entry of juveniles into the rearing area (Hartman et al. 1976; Rankin et al. 1979), and that forage organisms are large and numerous enough to stimulate efficient fry growth (LeBrasseur and Kennedy 1972; Hall and Hyatt 1974; Goodlad et al. 1974). Otherwise fry growth and survival will be curtailed (Gilbert and Rich 1927; Ruggles 1965; Meehan 1966) and smolts will either emigrate as small age 1. fish or hold-over another year (Barnaby 1944; Krogius 1961). Neither alternative is desirable; small size has been linked to reduced marine survival (Foerster 1954; Eicher and Rounsefell 1957; Ricker 1962; Barraclough and Robinson 1972; Hyatt and Stockner 1985), and protracted freshwater residence does not optimize production because freshwater survival is then reduced (Barnaby 1944; Burgner 1964; Johnson 1965; Foerster 1968).

The quantity and quality (e.g., age and size) of smolts are important indicators of lake rearing conditions and eventual production of harvestable adults (Merrell 1964; Meehan 1966). In this paper we provide experimental validation of smolt population responses to changes in the fry/forage base ratio. We do this by manupulating fry density to challenge rearing capacity, and nutrient input to increase rearing capacity. Our intent here is to establish differences between smolt populations from Alaskan lakes based on: (1) an empirical continuum of high to low juvenile: forage base ratios; and (2) non-forage based constraints to smolt production imposed by the freshwater environment. The design of enhancement and management strategies to produce the greatest number of harvestable adults may differ based on recognition of the freshwater limits to smolt production.

STUDY LAKES DESCRIPTION

Systems studied in this program included both coastal and interior lakes over a distance of 2 100 km from Kodiak

TABLE 1. Comparison of water-quality characteristics from oligotrophic Alaskan sockeye nursery lakes showing morphometry, water transparency, nutrient regimes, and primary production.

					May-October							
Lake	Typology	Year	Location	Elevation (m)	Total phosphorus (μg•L^{-1})	Total nitrogen (μg•L^{-1})	Chlorophyl-la (μg•L^{-1})	Euphotic zone depth (m)	Mean depth (m)	Surface area (km^2)	Annual pecipitation (cm)	Water residence time (years)
Tustumena	Glacial	1980	60°10′N 150°55′W	33	42.1	127.9	1.3	1.1	124.0	294.5	98	34.7
Crescent	Glacial	1980	60°22′N 152°56′W	183	6.6	313.2	1.1	8.1	23.0	16.5	169	0.8
Packers	Stained	1980	60°28′N 151°55′W	15	11.1	242.7	3.3	3.5	12.0	2.1	49	3.9
McDonald	Stained	1980	55°57′N 131°50′W	15	8.2	152.5	1.0	7.3	45.6	4.2	285	0.6
Hugh Smith	Stained	1979	55°06′N 130°40′W	12	4.8	173.6	2.0	5.5	61.0	3.2	374	1.1
Falls	Stained	1980	56°49′N 134°42′W	6	2.9	70.3	0.9	16.0	31.5	0.9	451	0.5
Upper Russian	Clear	1980	60°20′N 149°50′W	305	4.6	484.0	1.9	15.9	26.5	4.6	74	3.3
Larson	Clear	1984	62°20′N 149°53′W	186	6.9	796.1	1.0	9.7	16.4	1.8	59	1.9
Eshamy	Clear	1981	60°26′N 148°10′W	8	3.9	55.8	1.1	11.5	33.5	3.6	612	0.9
Leisure	Clear	1982	59°35′N 151°19′W	46	3.8	518.5	0.4	19.5	22.0	1.1	90	0.9
Tokun	Clear	1982	60°24′N 144°17′W	54	5.4	46.1	0.8	18.3	21.1	1.8	449	0.5
Hidden	Clear	1980	60°29′N 150°15′W	61	5.5	123.2	1.6	18.5	20.2	6.8	49	11.6
Karluk	Clear	1980	57°24′N 154°05′W	106	7.8	121.3	2.5	21.5	48.6	39.5	172	4.8

Island in the west to Southeast Alaska in the south (Table 1). All are classified as oligotrophic (Wetzel 1975) with seasonal (May–October) phosphorus (TP) levels averaging 2.9—11.1 μg•L^{-1}, water residence times ranged from 0.5 to 34.7 yr, and chorophyll *a* (chl *a*) levels varied between 0.4 and 3.3 μg•L^{-1} (Tustumena Lake is excluded because it has atypical TP values caused by rock phosphate bound in the glacial silt particles). The lakes range in area from 0.9 to 295 km^2 with mean depths of 12 - 124 m, surface elevations from 6 to 305 m, steep sides, and very small littoral zones. In addition, seasonal TN:TP ratios (by atoms) ranged from 255:1 to 19:1 indicating the importance of P in limiting primary production. The trophogenic zone depth (EZD) ranged from 1.1 to 21.5 m.

These lakes are dominated by either the small cladoceran *Bosmina longirostris*, the larger *Daphnia* spp. (almost always *longerimis*) or by the copepods *Cyclops columbianus* or *C. scutifer*. Usually when *Bosmina* densities are high, *Daphnia* densities are low, and when both species are rare, the herbivore role is assumed by the much larger calanoid copepods *Diaptomus pribilofensis* or *Epischura nevadensis*. The lacustrine fish communities are usually dominated by sockeye fry, but a few lakes have significant populations of threepine stickleback (*Gasterosteus aculeatus*).

Materials and Methods

The sockeye nursery lakes were surveyed at 3-wk intervals during the ice-free period, and 1-3 times during the winter period annually. Physical data included lake temperature and light penetration on at least two permanent stations. Lake temperature profiles were measured using a YSI temperature/dissolved oxygen model 57 meter. Recordings were at 1 m increments from the surface to 5 m, at 2 m increments from 6 to 12 m, and at 10 m increments from 20 to 50 m. The algal light compensation point or euphotic zone depth (EZD) was defined as the depth to which 1% of the subsurface PAR [photosynthetically active radiation (400–700 nm)] penetrates (Schindler 1971), and was measured using a Protomatic submersible photometer. The EZD and lake surface area (km^2) were used to calculate the euphotic volume (EV) or the magnitude of the trophogenic zone. A unit of euphotic volume is defined as 10^6 m^3 of the trophogenic zone.

Lakes were sampled for the algal nutrients nitrogen (N), phosphorus (P), silicon (Si), and carbon (C), and other epilimnetic and mid-hypolimnetic water quality parameters. All chemical and biological samples were analyzed by methods detailed in the Alaska Department of Fish and Game limnology manual (Koenings et al. 1987). In general, filterable reactive phosphorus (FRP) was analyzed by the molybdate blue-ascorbic acid method of Murphy and Riley (1962) as modified by Eisenreich et al. (1975). Total-P was determined by the FRP procedure after persulfate digestion. Nitrate and nitrite were determined as nitrite, after Stainton et al. (1977), following the cadmium reduction of nitrate. Kjeldahl nitrogen and ammonium analyses were according to Stainton et al. (1977) using the phenolhypochlorite methodology after and before digestion, respectively. The reactive silicon analysis followed the procedure of Strickland and Parsons (1972) while alkalinity levels were determined by acid titration (0.02 N H_2SO_4) to pH 4.5 using a Corning model 399A specific ion meter.

Algal standing crop was estimated by chl *a* analysis after the fluorometric procedure of Strickland and Parsons (1972). We used the low strength acid addition recommended by Reimann (1978) to estimate phaeophytin. Water samples (1-2 L) were filtered through 4.25 cm GF/F filters to which 1-2 mL of a saturated $MgCO_3$ solution were added just prior to completion. The filters were then stored frozen in separate plexislides for later analysis. Primary productivity (rate of carbon uptake) within the euphotic zone was determined with carbon -14 isotope experiments using three incubation depths i.e., surface (1 m), mid-euphotic, and the light compensation point. We utilize the light–dark bottle technique of Saunders et al. (1962) using 2–4 stations per lake with 6–7 sampling dates over the May–October period. Replicate clear and lightproof bottles containing 100 mL of lake water were labeled with 5.2 μ Curies (192 KBg•mL^{-1}) of $NaHC_{14}O_3$ and incubated in situ 4–6 h. Samples were fixed with Lugol's acetate solution and filtered through a 2.5 cm GF/F filter. Filters were stored frozen in 20 mL polyethylene vials. Prior to analysis, filters were thawed, acidified, and suspended in a toluene based scintillation cocktail. Algal carbon incorporation was quantified using a Packard model 3255 scintillation spectrometer. Volumetric uptake rates (mg C•m^{-3}) were calculated after Saunders et al. (1962), and day rate estimates (mg C•m^{-3}•d^{-1}) were determined using the cumulative percent time productivity curve of Vollenweider (1965). Mean daily rates were determined from integrated areal productivity time plots.

Zooplankton were enumerated from paired 50 m or bottom to surface vertical tows using either a 0.2 or 0.5 m diameter, 153 μm mesh conical zooplankton net. The net was pulled at a constant 1 m•S^{-1}, and washed well before removing and preserving the organisms in 10% neutralized formalin. At least two stations per lake were sampled 6–8 times during the open water period. Identification within the genus *Daphnia* was acccording to Brooks (1957); *Bosmina* after Pennak (1978); and copepods after Wilson (1959), and Yeatman (1959). Counts were triplicated 1-mL subsamples, taken with a Hensel–Stempel pipette, in a 1-mL Sedgewick–Rafter cell. Length of the individual zooplankters was obtained by counting at least ten individuals along a transect in each 1-mL subsample. Zooplankters were measured to the nearest 0.01 mm.

Lakes were enriched with a liquid nitrogen and phosphorus fertilizer having an atom ratio of > 18:1. Phosphorus was introduced as inorganic phosphate while nitrogen was in a mixture of one-third each of ammonium, nitrate, and urea. The fertilizer was applied as a 1:1 mixture of product and epilimnetic water delivered from a spray bar mounted across the stern of a boat. The upper end of the lake received an amount calculated not to exceed 90% of critical phosphorus loading as defined by Vollenweider (1976). Lakes were stocked with 0.2–0.3 g sockeye fry during June. The brood stock was from Tustumena Lake and eggs were taken in the fall before stocking, and incubated over winter. Emerged fry were fed medicated food for a period of 10 days prior to release.

Sockeye juveniles were counted and recorded with a 70 KHz Simrad EYM echosounder and Sony cassette recorder using a downward-looking 11-degree transducer suspended from the bow of a boat. Open water trawls with a 2 × 2 m tow net were used to capture juveniles for stomach content analysis and to verify hydroacoustic estimates. Paired cross-sectional tows were conducted along the entire longitudinal axis of the lake except in diel studies where single cross-sectional transects were conducted. The Ivlev (1961) electivity index (EI) was used to compare fish feeding habits with the availability of potential food organisms. Stomach contents were collected by gastric lavage, stored in 10% neutralized formalin, and identified and enumerated as described earlier for zooplankton samples. The EI has a range of −1 to +1, with negative values indicating avoidance, or inaccessibility of a prey item, zero indicating random selection, and positive values indicating active selection.

Total smolt counts or estimates (± 95% confidence intervals) were made at smolt fences (Litchfield and Flagg 1987), by timed subsampling (Lebida 1984), calibrated fyke nets (Flagg 1983), or inclined plane traps (Kyle 1983). Trap capture efficiency at various flow regimes was determined by a mark and recapture technique (Rawson 1984) using Bismark-Brown stained smolts. Throughout the migration, smolts were subsampled for age, length, and weight and determinations were made before processing. Sizes were weighted by the within period population size to give mean overall lengths and weights. Individual snout–tail fork lengths were measured to the nearest 1 mm while weights were determined to the nearest 0.1 g. Ages were read from projected acetate card scale impressions using a microfiche projector. In comparing smolt populations, we assumed that subject only to the biological limitations of the stock, size could range from small to large, irrespective of the length of the rearing period, geographic location, or point in history.

Adult sockeye were enumerated using picket weirs or Bendix side-scanning sonar and species composition was estimated from fish-wheel catches (e.g., King 1984). Sockeye were subsampled throughout the migration to determine fecundity, sex, length, weight, and age. Harvest rates were calculated from beach, vessel, and cannery samples during the fishery, and stocks were identified by scale pattern analysis (Cross et al. 1985). Ages were determined by the method of Clutter and Whitesel (1956). Total adult production and estimates of ocean survival by brood year were estimated from the foregoing data.

Results and Discussion

SMOLT POPULATION CHARACTERISTICS

Because two of the most variable smolt (S) population characteristics are mean length (SL) and mean weight (SW), we compared mean sizes for populations of age 1., 2., 3., and 4. smolts from lakes located throughout Alaska (Fig. 1). We found that during the 1975–85 period, mean population lengths ranged from 55.8 to 200.0 mm while weights ranged from 1.4 to 83.9 g. Overall, comparing SL and SW from 68 lake-year smolt populations (22 lake systems: four age classes) resulted in a single, highly significant relationship (Log SL = 1.71 + 0.31 log SW; r^2 = 0.99) indicating populations had virtually identical length–weight relationships. Moreover, inter-lake age classes were not discretely sized because size ranges overlapped age classes. There was a tendency for larger-sized smolts to be of greater age.

The curvilinear SL–SW relationship of Fig. 1 suggests a threshold or minimal smolt weight for Alaskan sockeye smolts at 2.0 g. We found only two instances of populations with smolt mean weights less than 2.0 g. They were 1.4 and 1.5 g, respectively. Further review of the extensive pre-1968 smolt information (64 lake-years) of Foerster (1968) and Rounsefell (1958), combined with the 53 lake-years summary of Hyatt and Stockner (1985) revealed only one or two Canadian lake systems producing smolts weighing substantially less than 2.0 g. In fact, our regression analysis of SL–SW data from Foerster (1968) resulted in a relationship (Log SL = 1.68 + 0.32 Log SW; r^2 = 0.98) indistinguishable from that in our own recent SL–SW data. Moreover, Foerster (1968) listed a minimal Canadian smolt population size of 2.0 g from the glacial Owikeno Lake (Foskett 1958). (The <2.0 g smolts described by Hyatt and Stockner (1985) were from several discrete samples which may not have represented entire populations.) Thus, the preponderance of our smolt information suggests that for most purposes a

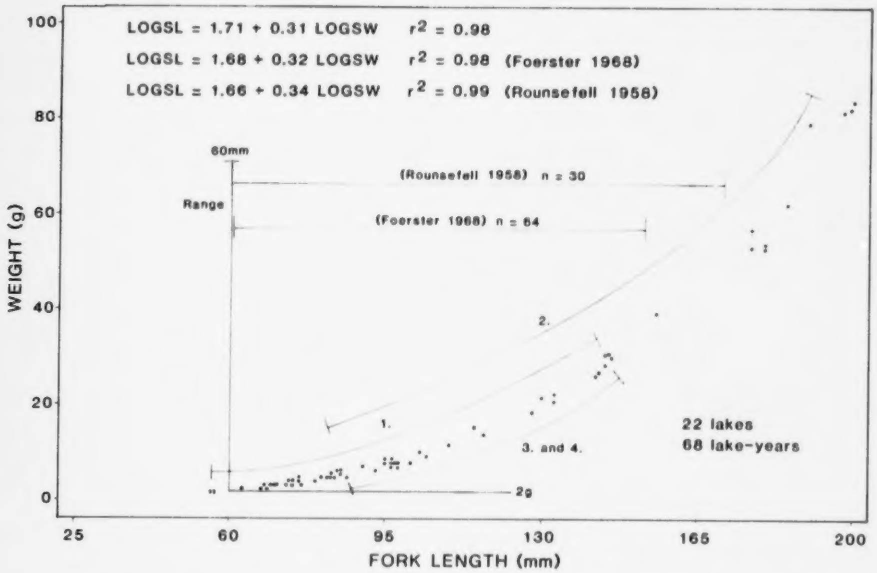

FIG. 1. Relationship between mean lengths (plus ranges) and weights of age 1., 2., 3., and 4. sockeye smolt populations from 22 Alaskan Lakes taken over 68 lake-years compared to similar ranges in smolt length calculated from Rounsefell (1958) and Foerster (1968). The non-transformed relationships are shown, with equations for log-log transformations, and minimal or threshold smolt population mean length (60 mm) and weight (2 g).

population mean of 2.0 g can be considered a threshold smolt size for both Canadian and Alaskan sockeye stocks.

The mean and range in lengths, and the 95% confidence limits of the mean corresponding to a 2.0 g threshold weight can be calculated from the length-weight equation of Fig. 1. i.e., Log SL = 1.71 + 0.31 Log SW; $r^2 = 0.98$. This yields a mean threshold length of 63 mm (range 60–65 mm), and through analogous calculations a mean threshold weight of 2.0 g (range 1.8 - 2.2 g).

REARING VERSUS RECRUITMENT LIMITS TO SMOLT PRODUCTION

We grouped lakes according to numbers of sockeye fry per lake unit (population density) and lake fertility (capacity to produce suitable forage). Production in these two groups of lakes is described and subdivided as follows:

A. Recruitment limited (low initial input and density of fry)
    1. Escapement limited (density independent)
    2. Spawning area limited (density independent)
B. Rearing limited (poor lacustrine conditions or fry-forage interaction)
    1. Forage limited
        a. Poor quantity and quality of forage base (density dependent)
        b. Poor spatial/temporal concurrence of fry and forage (density independent)
    2. Environment limited
        a. Unfavorable temperature regime (density independent)
        b. Short growing season (density independent)

This classification indicates that rearing limitation can be either forage or environment based or both, that forage limitation can be density dependent or independent; and that density independent growth can be either recruitment or rearing limited.

Lakes in category A. (subhead 1. or 2.) were found to produce above threshold sized >60–65 mm (>2.0 g), and essentially all (>85%) age 1. smolts. That is, small numbers of fry, given an adequate forage base, were able to vastly exceed the smolting size-threshold (they produced up to 30 g smolts) in one growing season. These systems produced spawning area, or escapement limited sockeye smolt populations. In contrast, category B. lakes (subhead 1. or 2.) consistently produced <85% age 1. smolts or an increasing proportion of age 2. or even age 3. smolts. They either contained above optimum numbers of fry for the existing forage base or forage which was not continuously available i.e., neither spawning areas nor escapement levels were limiting. Forage (B.1.) and environment (B.2.) limitations can effect smolt populations in similar ways (e.g., low temperatures can affect growth directly, or affect them indirectly via their food supply). However, we can differentiate between category B.1.a. and other rearing limited lakes i.e., between density-dependent and density-independent rearing limitation, on the basis of smolt numbers. Density-dependent forage limitation was indicated when a lake system produced ~85% age 1. threshold sized smolts in one growing season. In such instances, either naturally produced or stocked fry did not exceed lake carrying capacity. Thus, significantly, the numbers of threshold-sized smolts from B.1.a. systems can be used to estimate the forage based rearing capacity of nursery lakes for sockeye salmon juveniles.

SMOLT POPULATION RESPONSES TO FRY DENSITY MANIPULATIONS

Because we found a continuum in smolt population lengths and weights (Fig. 1) across a variety of lake types (Table 1) from the 1920's to the present, we reasoned that smolt characteristics may not be system dependent, but could arise from differences in fry density. To test this, we needed to accurately determine total numbers of juveniles rearing in spring, the smolts produced and their mean length, weight, and age. We chose as a whole lake experimental unit, Leisure Lake, which is typical of Alaskan sockeye systems (Table 1) except for having a physical barrier to adults, but not smolts, on the outlet stream. The lake was stocked annually, in early June, with known numbers of fry; and the resultant smolt populations (Table 2) and adult returns to the outlet stream were accurately counted and sampled.

We began in the spring of 1980 with a stocking of nearly 5 000 fry•ha^{-1} (Johnson 1965) which produced 240 658 age 1. smolts having a mean length of 97 mm and a mean weight of 8.0 g. We doubled the stocking density to nearly 10 000 fry•ha^{-1} in 1981, and in 1982 there were 77% age 1. smolts accompanied by a few age 2. holdovers from the 1980 plant. Although most of the 1982 smolts were age 1., their size decreased dramatically and averaged 4.0 g and 79 mm. In 1982 we added an additional 5 000 fry•ha^{-1}, which created a density of 15 000 fry•ha^{-1}, and in 1983 and 1984, respectively, observed a nearly 50% further decrease in weights of both age 1. and 2. smolts (2.2 g and 3.6 g). However, even at this higher density, most smolts (87%) still migrated at age 1.

The 1982 density produced age 1. smolts of mean size 2.2 g and 67 mm, and we felt confident that one additional fry increment would test our concept of a minimal or threshold size for rearing limited sockeye juveniles. The stocking density was therefore increased to 20 000 fry•ha^{-1} in 1983 and the resultant age 1. smolts again decreased in mean size, but only by 0.4 g (18%) reaching 1.8 g and 60 mm. This decrease compares to a 5 g (50%) decrease from 1981 to 1982, and 1.8 g (41%) decrease from 1982 to 1983. Thus, equivalent yearly increases in spring fry plants produced progressively smaller age 1. smolts, but the annual size decreases diminished as the smolts approached threshold size. The 1985, age 2. smolts were still substantially larger (3.4 g) than the threshold size, which indicated that, while holding over, they had grown in both years of lake residence but not rapidly enough to emigrate after one year. Finally, in 1984, we replicated the 1983 stocking with a density of slightly greater than 20 000 fish•ha^{-1}. The resulting age 1. smolts (1985) remained virtually equivalent in size to those in the 1984 outmigration i.e., the age 1. smolts remained at the smolting threshold.

As the number of juveniles stocked into Leisure Lake increased, smolt size changed in a manner consistent with increased intraspecific competition for food or density-dependent growth. That is, increasing numbers caused an ever increasing pressure on the forage base of the lake. As less and less food was available, juvenile growth rates presumably decreased, resulting in smaller and smaller age 1. smolts until a threshold size was reached. We found a highly significant negative relationship (Log SW = 4.98 - 1.09 log SD; $r^2 = 0.99$) between fry stocking densities (SD) and the resultant mean weight of age 1. smolts (SW). Accompanying the decrease in age 1. smolt weight was a decrease in lacustrine juvenile survival (FWS) described by the relationship: FWS = 58.62 - 0.0023 SD; $r^2 = 0.98$ (Fig. 2). Thus, increased juvenile densities (recruitment) reduced both the size of age 1. smolts and their lacustrine survival, presumably by slowing fry growth rates (Johnson 1965; Narver 1966). Rogers (1979) has also shown that the growth achieved by juveniles rearing in Lake Aleknagik, Alaska, is highly correlated with smolt size in the following spring.

TABLE 2. Brood-year population characteristics of Leisure Lake sockeye smolts showing a shift to smaller and older smolts during fry stocking, and to larger smolts following nutrient enrichment of the epilimnion.

Stocked Fry (millions)	Smolt year	Smolts					
					Size		Biomass
		Numbers	Age	(%)	(mm)	(g)	(kg)
0.5	1981	240 658	1.	97	97	8.0	1 925
	1982	6 390	2.	3	117	13.2	84
	Σ	247 048		100			2 009
1.0	1982	313 112	1.	77	79	4.0	1 252
	1983	91 727	2.	23	97	7.0	642
	Σ	404 839		100			1 894
1.5	1983	325 214	1.	87	67	2.2	716
	1984	47 670	2.	13	76	3.6	172
	Σ	372 884		100			888
2.0	1984	179 330	1.	58	60	1.8	323
	1985	131 815	2.	42	75	3.4	448
	Σ	311 145		100			771
2.1	1985	46 313	1.	24	62	1.8	83
	1986[a]	150 400	2.	76	111	11.2	1 685
	Σ	196 713		100			1 768
2.0	1986[a]	225 600	1.	—	87	5.1	1 151

[a] Results subsequent to nutrient enrichment in 1985.

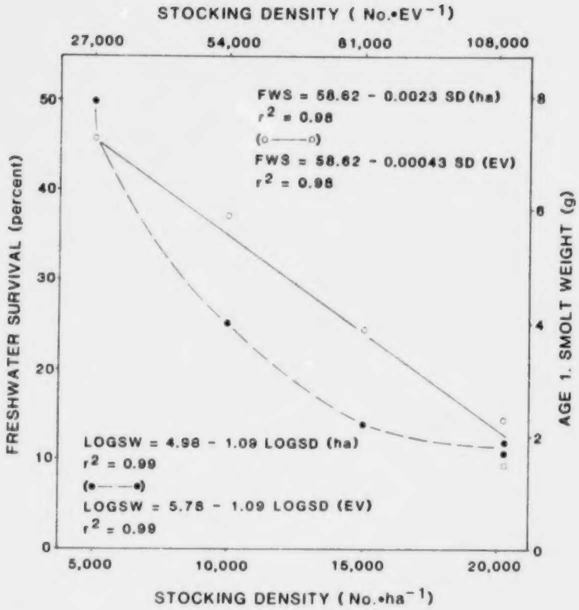

FIG. 2. Comparisons of brood-year fry to smolt survival (FWS) and the weights of age 1. smolts, and the stocking density (SD) of sockeye fry expressed on the basis of surface area (ha) and euphotic volume units (EV) (see Table 2). The non-transformed inverse relationships are shown along with the equations of the log-log transformations.

Moreover, at juvenile densities above that which produce threshold sized smolts, the forage base was deficient and fry growth was too slow to produce even a small majority of age 1. smolts. Consequently, only the fastest growing fry were able to exceed the smolt size threshold in the first growing year and the remainder stayed in the lake for a second year. For example, at the stocking density of 20 000 fry•ha^{-1} in 1983, only 179 330 (58%) of the resultant smolts were age 1. and an additional 131 815 migrated at age 2. in 1985. Because of the large number of "holdover" fish in 1984, the additional 20 000 fish•ha^{-1} plant resulted in only 46 313 threshold sized age 1. smolts in 1985. In 1985, 74% of an estimated 178 000 smolts resulted from fry requiring 2 growing years before emigration and 77% of the smolts from the 1984 brood required 2 yr to reach threshold size. This progressive increase in juvenile densities caused resultant smolts to become smaller and older. These results are consistent with those of Barraclough and Robinson (1972) for smolts of Great Central Lake, Canada; and by Bergander (1985) for Chilkoot Lake, Alaska, where only the smaller growing sockeye fry of a brood remain in a lake for 2 yr.

Overall, smolt production in Leisure Lake suggests that at a stocking density somewhere between 5 000–10 000 fish•ha^{-1}, the population was recruitment (an A.1. system) rather than forage limited. However, at stocking densities above about 15 000 juveniles •ha^{-1}, growth became progressively rearing limited and the resultant smolt populations began to change. Apparently, the forage base was being challenged because the resultant age 1. smolts could not achieve threshold size in a single season (a B.1.a system). Indeed at the highest recruitment (20 000 fry•ha^{-1}), not only were the resultant age 1. smolts held to the threshold size, but because of extremely high intraspecific competition for food a much larger number "heldover", i.e., brood age structure shifted to a preponderance of age 2. smolts (Table 2).

SMOLT POPULATION RESPONSES TO FERTILITY MANIPULATIONS

The purpose of the Leisure Lake experiment (up to the 1985 stocking) was to manipulate juvenile densities in an environment of natural autochthonous production of forage organisms in order to assess changes within the smolt populations. Our second experiment was to manipulate autochthonous forage production while attempting to keep juvenile recruitment constant. Again we hoped to measure any changes in the resultant smolt populations. However, for nutrient enrichment of the epilimnion to change smolt population characteristics, fry growth rates need be forage limited. That is, before treatment the system should produce a majority of age 2. smolts or threshold sized age 1. fish (a B.1.a. system).

From 1981 to 1984, escapements to Packers Lake did not vary greatly in number (range 12 904 – 18 403). Thus, the potential fry recruitment was similar in four consecutive years but the size of the 1980 escapement producing the 1981 age 1., 1982 age 2., and 1983 age 3. smolts was unknown. Prior to the first (1983) fertilization, we identified preferred forage items (Fig. 3) as described above and used the electivity index (EI) to compare frequency of capture of particular zooplankters with the frequency of that food item in the zooplankton community. Food preferences of fish in two tows (24 and 42 fish, respectively) were very similar indicating a representative subsampling of the fish. Stomach contents showed that the fry were not selecting zooplankters of large body size exclusively, but tended to single out particular species within a preferred size range, particularly from 0.40 to 1.00 mm (EI = 0.37). This occurred even though smaller (EI = −0.50) and larger (EI = −0.54) forms were not only present, but, in the case of the larger forms, present in greater densities (Fig. 4). The reason for the negative electivity indices for the larger body-sized zooplankters was that most of them were evasive copepods (e.g., *Cyclops* EI = −1.00), or less accessible (*Diaptomus* EI = −0.39). The major and preferred forage during both the spring (7 July) and late summer (31 August) periods as shown by both the number consumed and a consistently positive electivity index were *Bosmina* and *Daphnia*. Merrell (1964), Narver (1970), Goodlad et al. (1974), and Jaenicke et al. (1980) also found cladocerans to be preferred forage item for sockeye fry. Sockeye cannot effectively feed on zooplankters <0.40 mm in size, and as expected we found the negative EI for these forage items even though this small size category is dominated by the preferred cladoceran *Bosmina*. The inability of fry to crop these small organisms allows *Bosmina*, in particular, to remain as part of the zooplankton community even in the face of intense sockeye predation pressure.

Each summer, 1983–85, Packers Lake was fertilized, and the first macro zooplankters to respond were the herbivores *Bosmina* and *Daphnia*. The pre-fertilization seasonal mean cladoceran densities of 38 000/m^2 (n=28 samples) were

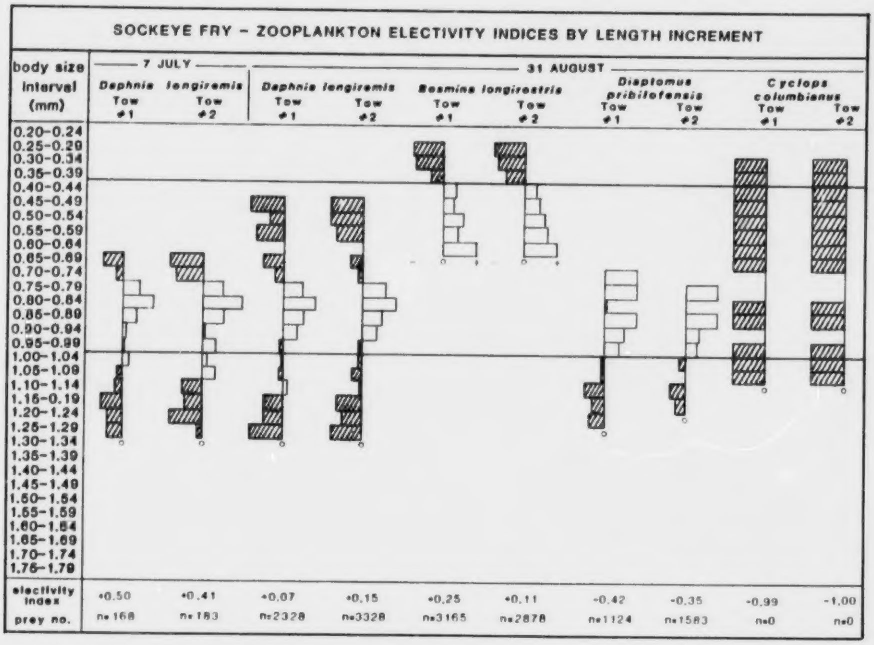

FIG. 3. Number of zooplankton consumed, along with electivity indices for each zooplankter, and 0.05 mm length interval within each zooplankter's overall size range. (Samples obtained from paired catches of limnetically rearing sockeye fry.)

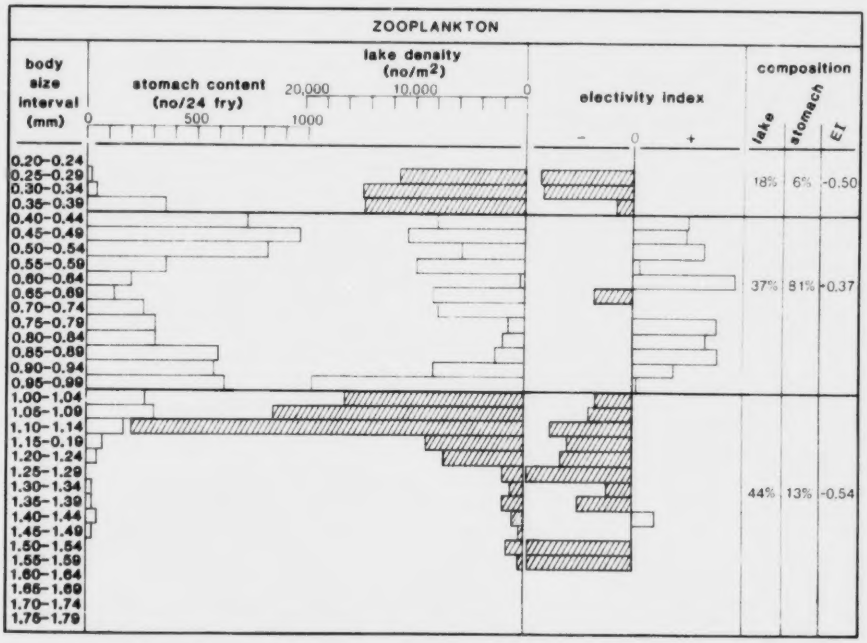

FIG. 4. Size distribution and numbers of zooplankters occurring concurrently in Packers Lake and the stomachs of 24 sockeye fry obtained from tow-net catches. Also presented are electivity indices (EI) by 0.5 mm body-size intervals, and both the composition and EI for a selected body-size range within the overall size range of the zooplankton community.

enhanced to 72 000/m^2 after fertilization in 1983 (n=28), and to 54 000/m^2 in 1984 (n=26); and their body-sizes increased. For example, the average body size of *Daphnia* increased from 0.75 mm prior to fertilization to more than 0.90 mm during the second year of enrichment. Concomitant with the increased density and body-size of preferred forage items, we observed a growth response in smolts emigrating after fertilization. The average size of age 1. smolts increased to 11.1 g, constituting a doubling in weight over smolts emigrating before nutrient enrichment (Table 3). The age 2. smolts, after an equivalent period of 12 mo of enhanced rearing, increased by 75% to 13.1 g, and the age 2. smolts in 1986, which reared for 2 yr under enhanced conditions, grew to a mean size of 26 g. On average, age 2. smolt weights increased to nearly three times those of the pre-fertilization period. Age 3. smolts showed even more dramatic growth by doubling in weight from 11.6 to 25.6 g after 1 yr, nearly quadrupling from 11.6 – 41.0 g after 2 yr, and reached 50.5 g in a full 3 yr of enriched rearing.

Along with increases in smolt size, associated with the years of lake enrichment, we saw a downward trend in age 2. smolt production i.e., a shift in age structure. Prior to fertilization an average of only 18 522 or 5% of the smolts emigrated from the lake at age 1. and 94% were age 2.. After fertilization, an average of 35% emigrated at age 1. and 61% at age 2.. Presumably, the increase in preferred forage items for the sockeye fry, or more specifically the increase in the forage base/fry ratio, caused fry to grow faster and emigrate as younger, larger fish. Nelson (1958) found analogous changes in the smolt population in Bare Lake, Alaska, and related larger sizes in three smolt age classes to increased photosynthesis caused by fertilizer additions.

At Packers Lake the potential juvenile recruitment as indexed by adult escapement levels was fairly constant but the actual number of fry rearing in the lake in spring was unknown. However, at Leisure Lake we could control the numbers foraging (except for holdovers from the previous broods) because the outlet barrier precludes natural spawning. To test the effect of nutrient enrichment on juvenile sockeye growth in a rearing-limited lake with a known number of spring recruits, we added 2.1 million juveniles (~ 20,000 fish•ha^{-1}) for a third consecutive year (1985) to Leisure Lake, and simultaneously added fertilizer (Table 2). The resulting production (i.e., larger and younger smolts) was consistent with results in both Packers and Bare lakes. After fertilization 11.3% of the planted juveniles emigrated as age 1. smolts at an average of 87 mm and 5.1 g. This compared with an average of 5.6% of the planted juveniles emigrating at mean sizes of 60–62 mm and 1.8 g in the two years immediately prior to fertilization (see Table 2). In addition, the size of post-fertilization age 2. smolts increased to 111 mm and 11.2 g compared to 75 mm and 3.4 prior to fertilization.

In essence, changes in both Leisure and Packers lakes smolt population characteristics in response to increased forage through fertilization contrasted sharply with changes among those from Leisure Lake in response to increased fry densities. Specifically, reduced intraspecific competition for food under fertilized conditions resulted in younger and larger smolts, whereas increased intraspecific competition under high stocking regimes resulted in older and smaller ones. Moreover, our Leisure Lake results demonstrate that smolt populations can reflect both rearing (a category B. system) and non-rearing (an A. system) limitation resulting from changes in fry density and lake fertility, i.e., the juvenile: forage base ratio.

SMOLT POPULATION RESPONSES TO ENVIRONMENTAL VARIABLES

Although the foregoing Leisure and Packers lakes stocking and fertilization experiments produced readily discernible changes in smolt populations, both the Tustumena Lake stocking and Hugh Smith Lake fertilization experiments provided less clear-cut results. However, when evaluated in the light of density-independent environmental variables, the smolt responses did demonstrate the importance of abiotic influences.

Tustumena Lake was initially stocked with 7.8 million fry (264•ha^{-1}, 24 000•EV^{-1}) in the spring of 1979 (Table 4), and received recruits from the 1978 escapement of 110 000 adults thus obtaining a two-fold escapement increase and three-fold stocking increase over the 1978–82 period. The combined fry populations produce from 1.32 to 15.42 million

TABLE 3. Pre- and post-nutrient enrichment characteristics of Packers Lake, sockeye smolts emphasizing the change to larger and younger smolts relative to the duration of post-fertilization rearing.

		Smolt											
		Age 1.				Age 2.				Age 3.			
	Smolt year	Number	Weight (g)	Length (mm)	Percent	Number	Weight (g)	Length (mm)	Percent	Number	Weight (g)	Length (mm)	Percent
Pre-Enrichement	1981	—	3.4	74	—	—	7.6	98	—	—	—	—	—
	1982	24 320	4.2	78	5	462 080	5.4	88	95	0	—	—	—
	1983	12 723	7.9	96	5	234 094	9.4	104	92	7 634	11.6	113	3
	Mean	18 522	5.2	83	5	348 087	7.5	97	94	3 817	11.6	113	3
Post-Enrichment	1984	36 970^{a}	8.8	92	22	129 395^{a}	13.1	113	77	1 680^{a}	25.6	123	1
	1985	43 200^{a}	8.5	97	20	157 680^{b}	21.2	132	73	15 120^{b}	41.0	165	7
	1986	109 562^{a}	16.0	120	63	57 371^{b}	26.0	140	33	6 954^{c}	50.5	175	4
	Mean	63 244	11.1	100	35	114 815	20.1	128	61	7 918	39.0	154	4

[a] One year under nutrient enhanced rearing.

[b] Two years under nutrient enhanced rearing.

[c] Three years under nutrient enhanced rearing.

TABLE 4. Population characteristics of Tustumena Lake sockeye smolts during increased fry stocking from 5.2 million in 1980 (177 fry•ha^{-1}), to 17.1 million in 1984 (581 fry•ha^{-1}) and concomitant increases in escapement.

Potential Spawners	Stocked fry (millions)	Smolt year	Smolts Numbers (millions)	Age	(%)	Size (mm)	Size (kg)	Biomass
—	None	1979	—	1.	—	—	—	—
		1980	0.09[a]	2.	—	86	4.7	423
		Σ	—					
110 000	7.8	1980	0.91[a]	1.	69	68	2.7	2 457
		1981	0.41	2.	31	88	5.1	2 091
		Σ	1.32					4 548
149 000	5.2	1981	1.89	1.	65	70	2.8	5 292
		1982	1.02	2.	35	82	4.8	4 896
		Σ	2.91					10 188
181 000	8.8	1982	4.08	1.	76	69	2.9	11 832
		1983	1.29	2.	24	83	4.0	5 160
		Σ	5.37					16 992
247 000	15.9	1983	6.48	1.	69	70	2.9	18 792
		1984	2.86	2.	31	84	5.2	14 872
		Σ	9.34					33 664
169 000	16.9	1984	11.44	1.	74	73	3.3	37 752
		1985	3.98	2.	26	84	4.3	17 114
		Σ	15.42					54 866
200 000	17.1	1985	12.62	1.	85	70	2.6	32 812
		1986	2.22	2.	15	84	4.7	10 434
		Σ	14.84					43 246
221 000	16.4	1986	5.18	1.	—	69	2.8	14 504

[a] Conservative estimate from the initial year of sampling.

smolts annually. During the 6 yr of increasing fry numbers we saw very little change in smolt population characteristics. That is, from the 1978 brood-year low smolt production to the 1982 brood-year high production age composition remained at 76–82% age 1. with mean weights from 2.6 g to 3.3 g only, and mean lengths from 69 to 73 mm. There were no discernible changes in age 2. smolt characteristics either. Their mean weight ranged only from 4.0 to 5.2 g, and mean length ranged from to 82 to 88 mm, well within the interannual variation which could be expected without enrichment.

Given the small size (near the smolting threshold) and relatively few Tustumena Lake smolts in the 1978 brood, we expected the increases reported above to cause a shift to predominantly age 2. smolts. However, the absence of appreciable brood-year (Table 4) or production-year (Fig. 5) age shifts coupled with the almost constant mean smolt size argued for a density-independent cause.

Some insight into the nature of density-independent production came from studies of fry growth relative to rearing temperatures in Hugh Smith Lake. These were undertaken because Hugh Smith smolts showed little size or age structure response to nutrient enrichment compared with smolts from both Packers and Leisure lakes.

That is, even though enrichment caused seasonal increases in both chl *a* and zooplankton densities, smolt population characteristics remained relatively unchanged. We therefore looked at the specific rearing location of the fry during May through October. Diel vertical patterns of fry migration, obtained by hydroacoustic surveys and compared with temperature profiles, revealed that a majority of the fry rarely migrated out of the 7°C isotherm. This suggested that temperature may be an important factor, controlling fry growth rates and resultant smolt sizes, independent of fry density. Peltz (1986), assuming food satiated growth, used the growth model of Iwama and Tautz (1981) to predict age 1. smolt size based on lake rearing temperatures and the length of the growing season. He found lake temperature in the rearing area to be an excellent predictor of smolt size (Table 5). Over 4 yr the predicted population mean weights of age 1. smolts were all within ± 10% of the observed, while the number of age 1. smolts varied six-fold from about 45 000 to nearly 294 000.

These Hugh Smith Lake results may suggest a similar density-independent mechanism in Tustumena Lake (B.2.a. systems). Since Tustumena receives large volumes of glacial meltwater, cool temperature regimes and a limited forage base may influence smolt size (Koenings et al. 1986). Small smolts were also observed emigrating from both the glacially turbid Crescent Lake, Alaska (Kyle 1983), and the cold, silty Chilkoot Lake, Alaska (Bergander 1985). Ruggles (1965) suggested that the cold, unproductive water of glacially influenced Owikeno Lake, Canada, may be responsible for its unusually small sized (60 mm) smolts (Foskett 1958), and Goodlad et al. (1974) suggested that sockeye growth in glacially influenced Chilko Lake, Canada, was more associated with temperature than forage supply.

SMOLT POPULATION RESPONSES TO THE TIMING OF JUVENILE FORAGE PRODUCTION

Hidden Lake and Karluk Lake revealed further aspects of fry rearing that can structure smolt populations. Limnologically (Table 1) these two lakes are very similar though Karluk has somewhat higher levels of total P and subsequent-

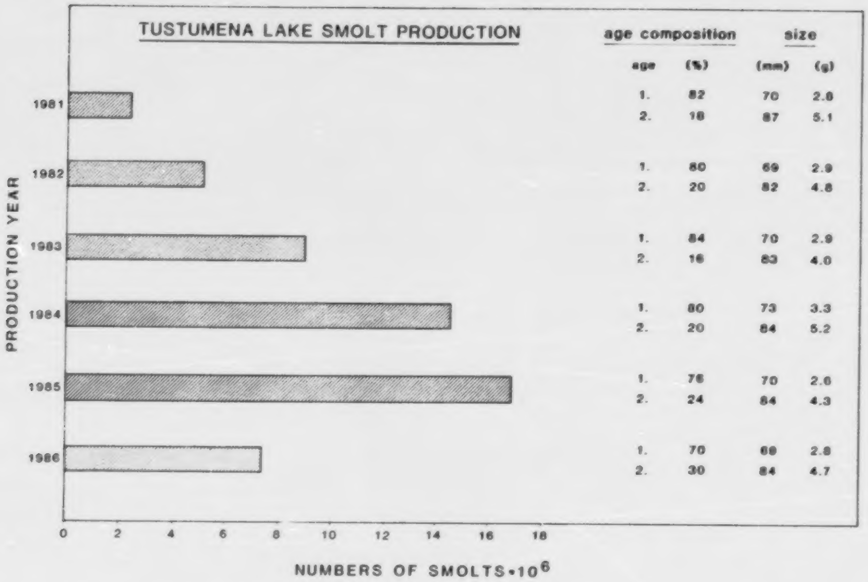

FIG. 5. Comparisons of total annual smolt numbers, age composition, and mean length and weight for Tustumena Lake sockeye smolts. Data are presented by production (calendar) year.

TABLE 5. Numbers of age 1. and 2. sockeye smolts migrating from Hugh Smith Lake in relation to both the observed and predicted weight of age 1. smolts. Predicted outmigrant weights were derived from observed juvenile rearing temperatures, rearing duration, and forage satiated growth after Iwama and Tautz (1981).

	Smolts				
Year	Age 1. (No.)	Age 2. (No.)	Age 1. Predicted	weight (g) Observed	Accuracy of prediction
1981	215 228	103 629	2.76	2.88	−4%
1982	53 789	36 536	2.72	2.68	+2%
1983	45 315	31 703	3.54	3.19	+10%
1984	293 653	31 716	3.54	3.57	−1%

ly a higher chl *a* content in summer. The species composition of the zooplankton, and the seasonal mean density of macro-zooplankton were also very similar (Fig. 6).

Recent parent year escapements to the Karluk system averaged 7 900 adults•km^{-2} compared to 2 200 adults•km^{-2} for Hidden Lake. Despite its 3–4 times larger escapements, Karluk produced an average of only 31 000 smolt•km^{-2} (range 21 000•km^{-2} – 52 000•km^{-2}) whereas Hidden L. produced 30 000 smolt•km^{-2} (range 24 000•km^{-2} – 35 000•km^{-2}). Karluk smolts of all ages average 14 g compared with 28 g at Hidden. Thus, both systems produce unusually large smolts, but Hidden consistently produced 93–99% (1981–84) age 1., whereas Karluk consistently produced 77–85% (1981–84) age 2. smolts. The critical question is: why does Karluk Lake produce predominantly age 2. and age 3. smolts when a lake of comparable production (Hidden Lake) produces predominantly age 1. smolts?

Since smolts of all ages from both lakes were well above the smolting threshold size, recruitment (fry estimated from number of adult spawners) was apparently not sufficiently large to challenge lake rearing capacity. Apparently, abundant forage exists at Hidden as the smolts were all large age 1. fish. However, similar forage densities at Karluk would forecast the production of mainly age 1. smolts there also. This does not occur and we believe the numerical dominance of the 2. and 3. age classes in Karluk Lake is partly explained by asynchrony in the seasonal timing of zooplankter abundance (Fig. 6) with fry entry into the rearing area. To test this belief, we partitioned the rearing period into two equal portions; an early period from May to July, and a later period from August to October. In Hidden Lake, zooplankton abundance is usually at a maximum by mid-May, with a lower peak occurring by the end of August. However, in Karluk, peak abundance is in the fall, typically during late September. Thus, in Hidden 65% of the total macro-zooplankters were produced prior to 1 August compared with only 37% in Karluk. Moreover, at Karluk only 6–36% of the seasonal biomass of the important cladocerans occurred in the early period. Foerster (1968) stressed that heavy mortality could occur if fry appear in nursery lakes when the important zooplankters are not readily available. Indeed, indications

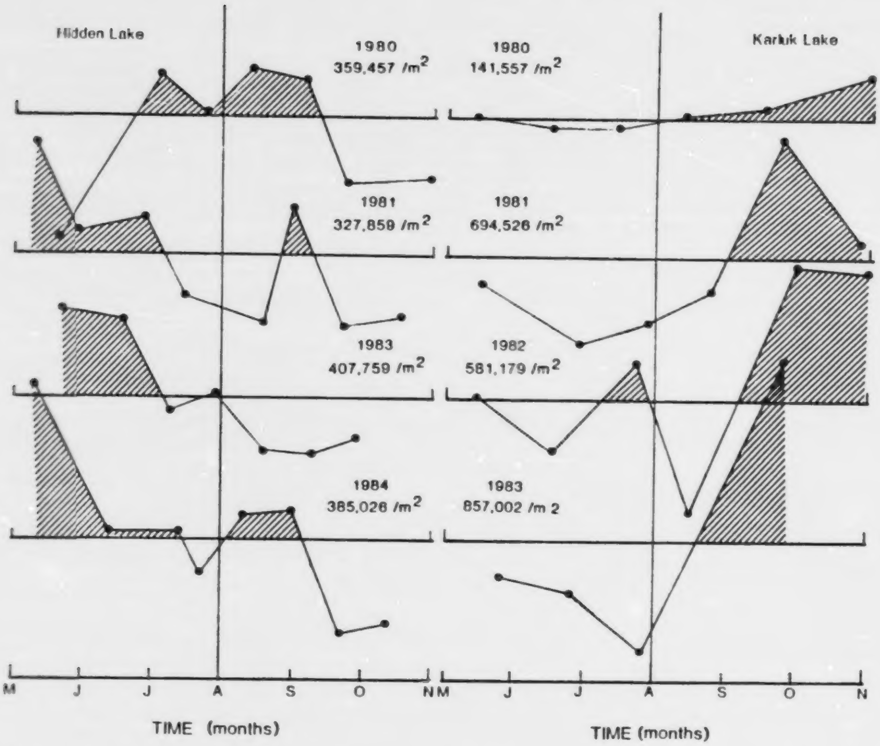

FIG. 6. Summary of the seasonal timing of highest zooplankter density during 4 yr at Hidden and Karluk lakes. The horizontal lines show mean May–October zooplankter density. Specific points represent differences between the period mean and the densities of all macro-zooplankters exclusive of rotifers and copepod nauplii.

are that on average Karluk Lake produces only 4 smolt•spawner^{-1} while Hidden Lake produces 14 smolt•spawner^{-1}.

Hartman et al. (1967) noted that fry from spring spawners emerge and migrate into Karluk Lake in April while fry from fall spawners emerge and migrate in late June or July. Our surveys indicate that limnetic temperatures at 20 m peak in September coincident with increasing macro-zooplankter density (Koenings and Burkett 1987). Thus, once in the limnetic area, fry may grow efficiently only during the brief 6-wk period just prior to fall–winter cooling and cease growing thereafter (Eggers 1978). A majority of the fry will not grow fast enough to reach smolt threshold-size within this short period and will be forced to remain in the lake for an additional year. However, close synchrony between fry entry (April) and zooplankter abundance (May) is characteristic of the majority of fry in Hidden Lake. Consequently, the Hidden smolt population reflects an abundant forage base with essentially all smolts emigrating from the lake at age 1. and an extremely large (~28 g) mean size.

Environmental variables (e.g., light, temperature) and in-lake nutrient cycles drive phytoplankton periodicity (Porter 1977), and, with temperature (Patalas 1975), determine both the timing and peak densities of herbivorous zooplankters. At Karluk Lake the coincident peaking of zooplankton densities and cool rearing temperatures in the late fall–winter period generates a density-independent response in the smolt populations (a B.1.b. system). This suggests that the large age 2. smolt component occurs not because of an overall low density of forage organisms, but because of their production timing (Koenings and Burkett 1987). This agrees with the findings of Hyatt and Stockner (1985), which indicated that zooplankton biomass does not by itself account for most variations in sockeye smolt sizes among lakes and years.

OCEAN SURVIVAL OF SOCKEYE SMOLTS

Assuming a positive relationship between smolt size and ocean survival, fry stocking densities and adult escapements can be used to regulate smolt numbers and sizes, and thereby optimize adult returns. The ocean survival of four age classes of sockeye smolts (average sizes ranging from 67 to 200 mm) from nine lakes (46 lake-years) may be expressed as a polynomial curve; $\text{Log } Y = -2.647 + 0.035 \times -0.000142 X^2$; $r^2 = 0.36$ (Fig. 7). Curve (A) has three main features: an ascending portion representing smolt sizes 67 – 110 mm, a point of diminshing return at 120 mm, and a descending portion from 125 to 200 mm. This suggests that smolt age has less to do with ocean survival than smolt size, but that increased size was correlated with increased survival, over a relatively small size interval. Even if we remove the largest (> 170 mm) age 2. Hidden Lake smolts, a polynomial curve (B) still provided the best fit ($r^2 = 0.42$). This curve retained the shape of curve (A), but was shifted slightly to the left resulting in a point of

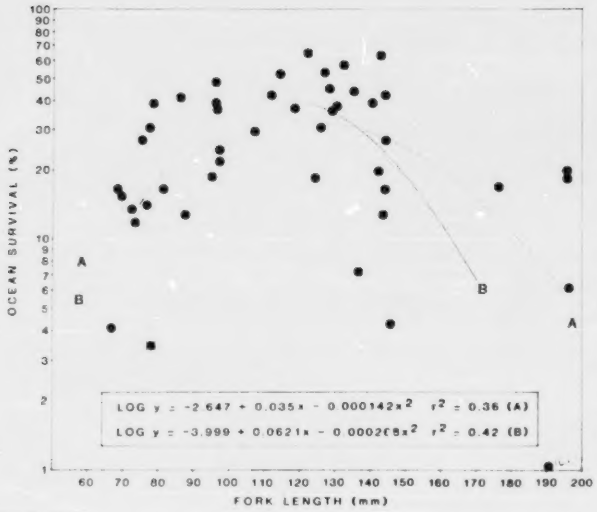

FIG. 7. The relationship between smolt length and mean survival for age 1., 2., 3., and 4. sockeye smolts from nine Alaskan lakes during 1962–1983. Included are glacial (Tustumena and Crescent), organically stained (Packers, Hugh Smith), and clear (Upper Russian, Larson, Leisure, Hidden, and Karluk) lakes. Curve A includes the smolt size range of 67 to 200 mm whereas Curve B includes smolt sizes from 67 to 170 mm i.e., the range of smolt sizes of Ricker (1962).

diminishing returns above a smolt body-size of 110 m. This is very near the (107 mm) breakpoint in Ricker's (1962) data covering the same smolt size range. Hyatt and Stockner (1985) recognized this same breakpoint and successfully fitted an angular transformation to Ricker's data.

Our data set emphasizes lakes in the more northern range, so it is not strictly comparable with Ricker's six-lake data set, which includes systems in the southern range of the species. Moreover, ocean survival of similar sized smolts may vary depending upon regional differences in estuarine fertility and turbidity, and how far smolts must travel to the ocean. In addition, neither stock specific smolt rigor nor accuracy in enumerating adult returns is consistent among data sets.

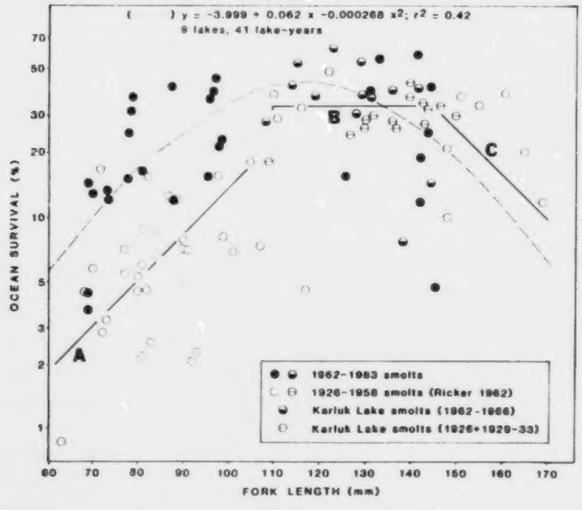

FIG. 8. Comparison of ocean survival of sockeye smolts from 1926 to 1958 (Ricker 1962) and 1962–1983. Dashed line represents the best statistical model for the smolt-size range of 67 – 170 mm for the later period whereas the solid lines (A, B, and C) were fitted by eye to the historical data presented in Ricker (1962).

Nevertheless, we think it useful to examine ocean survival patterns and estimate the upper limits possible from smolts of given size. Ricker's (1962) analysis and ours both show that ocean survival changes in similar non-linear fashion with increasing body-size (Fig. 8). Specifically, we found that a linear model using smolt length accounted for 36 and 44% of the variation in ocean survival up to 100 and 130 mm, respectively. Use of angular (i.e., arcsine) or log transformations increased the amount of variation explained by length, to 42 and 47%, respectively. However, beyond 130 mm increasingly angular transformations were required to maintain statistically significant relationships and only polynomial expressions were useful beyond 140–150 mm. That is, over the entire 67–200 mm range in body-size, linear and angular transformations resulted in non-significant relationships. Conversely, polynomial curves that incorporated a descending limb at higher smolt sizes provided a highly significant ($P<0.001$, *f*-test) relationship.

Our recent estimates of sockeye ocean survival rates suggest, on the whole, a higher survival than those of Ricker (1962), especially for fish emigrating in the size range of 67–110 mm (Fig. 8). However, a more pertinent comparison may be made if all fish are from the same lake system. We therefore used our Karluk stock ocean survival rates during 1962–66 and those of Ricker (1962) for 1926 and 1929–33. Our analysis suggested that survival rates were indeed somewhat higher in the more recent years even though the average size of Karluk Lake smolts has declined (see Koenings and Burkett 1987). This suggests that ocean survival rates of the recent period may, on average, be higher than those measured 30–50 yr earlier.

Prior to this study, the large age 2. sockeye smolts from L. Dalnee in the U.S.S.R. grew faster than those of any known American stock (Ricker 1962) including the unusually large sized age 2. and 3. Karluk smolts. Yet, four out of six Dalnee smolt broods had lower survival than was estimated for Karluk smolts. Ricker (1962) recognized this, but rather than hypothesizing a decline in ocean survivals of smolts > 140 mm in length, he thought that ocean survivals of such large fish should actually be higher.

Evaluation and Conclusions

Having experimentally demonstrated smolt population responses characteristic of recruitment-limited, A category (Hidden and Leisure lakes) versus rearing-limited, B category (Packers, Tustumena, Hugh Smith lakes) we were interested in comparing smolt numbers from lakes where juvenile sockeye growth was limited by the forage base alone i.e., category B.1.a. lakes. We sought an empirical relationship between primary productivity and smolt yield in a variety of nursery lakes where smolt population characteristics reflected forage-limited fry growth. Such a relationship could then be used to choose the appropriate enchancement strategy, i.e., lake enrichment or fry stocking.

PRIMARY PRODUCTIVITY (FERTILITY OF SOCKEYE NURSERY LAKES)

As photosynthesis is proportional to the solar energy and temperature at given depths, primary production in lakes having a narrow concentration of productivity-limiting nutrients (oligotrophic) would be highly sensitive to changes in light. As light penetration is progressively reduced by abiotic particles such as organic stain or glacial silt, areal rates of primary production in glacial, stained and clear-water lakes become a function of euphotic zone depth (EZD). Further, total limnetic production is dependent on both the EZD and upon the size of the lake area which we define as the euphotic volume i.e., trophogenic zone. Thus, we used units of euphotic volume (EV) to estimate the volume and fertility of sockeye nursery lakes (one unit of EV equals 1×10^6 m^3 of the trophogenic zone).

Comparisons of mean daily areal primary productivity (PROD) estimates (May–October) with the depth of the euphotic zone for a variety of lake types (Fig. 9), revealed a significant ($P<0.005$; *t*-test) relationship (PROD = 17.2 + 13.9 EZD; $r^2 = 0.81$). Interestingly, the slope of the regression equation indicated an across lake-type mean volumetric photosynthetic rate of 14 mg $C \bullet m^{-3} \bullet d^{-1}$. Thus, fertility of the studied Alaskan lakes is roughly constant. However, the areal photosynthetic rates of lake types are different, with systems having euphotic zones reduced by abiotic particles (glacial silt or organic stain) producing less.

SMOLT PRODUCTION (NUMBERS AND BIOMASS) IN RELATION TO LAKE FERTILITY

Having found a readily useable index (EZD) to areal photosynthesis in oligotrophic lakes, and defined relevant smolt population characteristics; we thought there should be quantifiable relationships between euphotic volume (EV) and smolt production (Table 6). In fact, both total smolts (SN) and total biomass (SB) were highly correlated with EV ($P<0.005$; *t*-test): ($SN = -42\,021 + 23\,010$ EV; $r^2 = 0.97$); ($SB = -130 + 81.22$ EV; $r^2 = 0.97$). However, because Tustumena's EV and smolt numbers far exceeded those in other systems, we applied Spearman's rank-correlation coefficient test and again found significant ($P<0.005$; *t*-test) correlation. There was no significant difference between simple means of numbers (23 000 smolts $\bullet EV^{-1}$) or biomass (81 kg$\bullet EV^{-1}$). Thus we could confidently forecast the numbers and biomass of smolts which would be produced by a given rearing limited population of sockeye juveniles when EV is known. In addition EV was found to normalize smolt production data more consistently than surface area corrections (Table 6). EV and km^2 gave respectively 3-fold and 15 fold ranges in numbers, and 7-fold and 16-fold ranges in biomass. In addition to reducing variability in smolt density estimates across lake systems, it gave much more consistent forecasts of smolt numbers and biomass (Table 7).

The value of EV is further illustrated by using independently derived data of Foerster (1954), and light penetration profiles (Ricker 1937; Goodlad et al. 1974) from Cultus Lake, Canada. We converted these authors' secchi disk (SD) readings to EZD using a formula developed for Alaskan lakes: EZD = 2.23 + 1.49 SD; $r^2 = 0.78$. The resulting seasonal mean EZD combined with the surface area of Cultus Lake gave an EV of $151 \bullet 10^6$ m^3 (EV unit = 151). Cultus age 1. smolt size records suggested that the system may have approached rearing limitation in both 1929 and 1941 and we calculated an average production in those years of 21 321 smolts$\bullet EV^{-1}$ (Table 6) quite similar to the average for Alaskan lakes.

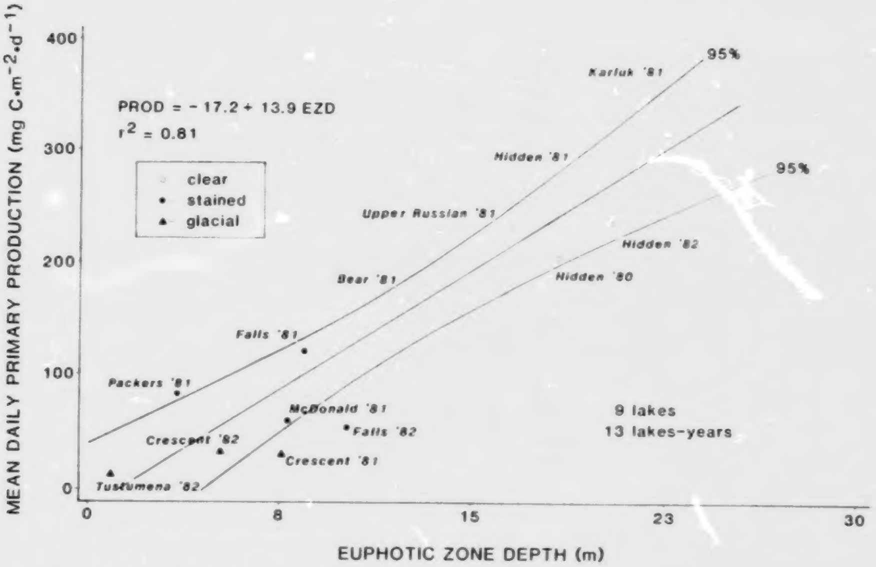

FIG. 9. Relationship of observed mean daily primary production (mg $C \bullet m^{-2} \bullet d^{-1}$) and euphotic zone depth (EZD) from May–October in nine Alaskan sockeye nursery lakes. Included are clear, stained and glacial lakes sampled during 1980–82.

TABLE 6. Sockeye smolt numbers and biomass from twelve rearing-limited (category B.) Alaskan, and one Canadian lake system. Glacial (no.'s 1-2), stained (3-7), and clear (8-12) lakes smolt production based on surface area (km^2), and euphotic volume (EV units). Lakes 1-3 are classified as B.2. systems (see text) while lakes 4-12 are classified as B.1. systems yet all are characterized by producing $<85\%$ age 1. smolts of approximately minimal or threshold (60-65 mm) size.

Lake	Smolt years	Mean total Smolt (No.)	Mean smolt biomass (kg)	Surface area (No./km^2)	Surface area (kg/km^2)	Euphotic volume (No./EV units)	Euphotic volume (kg/EV units)
1. Tustumena	1981-84	7 670 000	26 845	26 000	91	23 600	83
2. Crescent	1981-82	1 236 000	3 832	76 296	237	13 900	43
3. Hugh Smith	1981 & 1984	322 000	1 143	99 418	432	22 518	98
4. Falls	1982	125 000	360	131 579	355	13 158	38
5. McDonald	1982-83	1 250 000	2 010	297 619	479	39 682	63
6. Packers	1981-83	336 000	2 109	160 000	1 004	40 030	251
7. Black Bear	1982	16 500	48	67 901	198	16 975	49
8. Upper Russian	1978-79	940 700	6 679	204 500	1 452	13 633	97
9. Larson	1982-83	644 000	2 383	357 778	1 327	36 000	132
10. Eshamy	1982	1 395 000	4 464	387 500	1 240	27 353	80
11. Leisure	1983-84	333 363	968	303 057	880	16 837	49
12. Tokun	1983-84	438 350	1 201	243 528	667	17 534	48
13. Cultus	1928 & 1941	3 220 000	9 211	511 680	1 464	21 321	61

TABLE 7. Comparison of sockeye smolts produced from a hypothetical lake 50 km^2 in area with a euphotic zone depth of 1 m based on surface area and euphotic volume using regression equations and simple averages. To provide further comparison of the sensitivity of the analyses to individual systems, Tustumena and Crescent Lake smolts were sequentially removed from each analysis.

Model	Surface area (km^2) Numbers	Surface area (km^2) Biomass (kg)	Euphoric volume (units) Numbers	Euphoric volume (units) Biomass (kg)
Regression analysis				
All systems ($n=12$)	1 761 334	6 207	1 108 479	3 923
Minus Tustumena ($n=11$)	3 832 724	12 374	912 881	3 434
Minus Tustumena and Crescent ($n=10$)	12 943 645	52 671	1 027 286	4 402
System average				
All systems ($n=12$)	9 813 250	34 850	1 171 750	4 300
Minus Tustumena ($n=11$)	10 587 150	37 600	1 171 000	4 300
Minus Tustumena and Crescent ($n=10$)	11 264 400	40 150	1 218 600	4 500

BETWEEN LAKE COMPARISON OF CARRYING CAPACITY

Comparison of either fry density or smolt production from large, glacial Tustumena Lake with those from small, clear Leisure Lake (Table 1), demonstrates the need to consider lake fertility when comparing fish yields. This comparison of lakes is particularly relevant since the fry planted in Leisure Lake were taken annually from Tustumena Lake stock. We found that smolt characteristics were coupled to density-dependent fry growth in Leisure Lake (Fig. 2) whereas density-independent fry growth was responsible for the static smolt population characteristics of Tustumena Lake (Fig. 5). Such divergent population responses, given the same parental fry stock, argue that smolt characteristics may be shaped more by the rearing environment than by intrinsic stock properties.

Finally, using only lake size (surface area) to compare lake carrying capacity or smolt yield would suggest that Tustumena should produce less than 10% of the numbers and biomass of smolts that Leisure Lake does (Table 8). However, when the EZD, as well as lake size is considered, the two lakes are seen to have comparable production per EV. Thus, estimates of the carrying capacity or smolt yield of the two systems only correspond closely when EV is used as a fertility correction.

ADULT PRODUCTION IN RELATION TO SMOLT NUMBERS AND SIZE

We have stressed that smolt production involves two variables, lake fertility and numbers of fry, that can be largely independent of each other. When both are high, a lake system can produce a large biomass of smolts; when both are low, it will provide a very small one. However, in most systems, lake fertility is not always a direct function of the number of spawners so each variable fluctuates independently, and accounts for considerable yearly variation in smolt production (Foerster 1954). At the same time it is well known that adult returns can directly influence lake fertility (Krokhin 1967; Donaldson 1967; Richey et al. 1975) and by rearrang-

TABLE 8. Comparison of smolt numbers and biomass by production (calendar) year from Leisure (clear water) and Tustumena (glacial water) lakes using surface area (ha) to correct for lake size: and euphotic volume (EV units) to correct for lake size and carrying capacity. Leisure Lake fry originated from the Tustumena Lake stock.

	Numbers of smolts				Biomass of smolts (kg)			
	Surface area (ha)		Euphotic volume (units)		Surface area (ha)		Euphotic Volume (units)	
Year	Tustumena	Leisure	Tustumena	Leisure	Tustumena	Leisure	Tustumena	Leisure
1980	34	—	3 077	—	0.09	—	9	—
1981	78	2 292	7 077	12 154	0.25	18.3	23	97
1982	173	3 043	15 692	16 136	0.57	12.6	51	67
1983	275	3 969	24 923	21 047	0.84	12.9	77	68
1984	485	2 162	44 000	11 465	1.79	4.7	162	25
1985	563	1 697	51 077	8 996	1.69	5.1	154	27
1986	251	3 581	22 769	18 990	0.84	26.7	77	141
Mean	266	2 791	24 088	14 789	0.87	13.4	79	71

ing the data of Gadau (1966) we formulated a relationship between summer photosynthesis (mg C$\bullet$m^{-3}) and P increases (mg$\bullet$m^{-3}) derived from P imported in carcasses (CAR-P) by returning adult salmon in ten Bristol Bay lakes: (PHOTO = 1.26 + 0.830 CAR-P; r^2=0.78).

Smolt numbers and size are the primary determinants of numbers of adults which will return in the next generation, and at Leisure Lake a decrease in body-size from 97 to 67 mm, reduced ocean survivals of age 1. smolts from 40 to 4.4%, and changed adult returns from each stocking density (Fig. 10). Quite clearly the specific stocking density of 10 000 fry$\bullet$ha^{-1} (54 000$\bullet$EV^{-1}) produced the greatest adult return of over 1 600 fish$\bullet$ha^{-1} (8 700$\bullet$EV^{-1}). In contrast, when rearing-limitation was achieved, at a stocking density of 20 000 fry$\bullet$ha^{-1} (108 000$\bullet$EV^{-1}), Leisure Lake is expected to produce 375 adults$\bullet$ha^{-1} (2 000$\bullet$EV^{-1}). Because of the outlet barrier these adult production levels resulted without benefit of nutrients normally imported by spawners. To compensate we added nitrogen and phosphorus in 1985 at a level and atom ratio equivalent to a 50:50 catch/escapement of the 1984 return of 117 000 adults (Koenings et al. 1987). Smolt populations, resulting from equivalent additions of 20 000 fry$\bullet$ha^{-1}, compared before (1985) and after (1986) enrichment were completely different (Table 2). Age 1. smolt numbers increased nearly five-fold and mean weight increased three fold.

In contrast with density dependent Leisure Lake, density independent systems like Hugh Smith and Tustumena have a narrower range in smolt sizes (Tables 4 and 5) and reduced effects of size dependent ocean survival. In these systems increases in adults cannot be achieved by manipulating stocking density or lake fertility to increase smolt size; it can only be achieved through increased smolt numbers.

However, both types of rearing environment can be limited at smolt densities of 23 000$\bullet$EV^{-1} or biomass of 81 kg$\bullet$EV^{-1} (Table 6). We also find that long term adult sockeye population (ASP) is related ($P<0.005$; t-test) to nursery lake EV (ASP = −95 000 +2 498 EV; r^2 = 0.95) (Fig. 11) but not to surface area (ASP = 543 310 + 569.4 km^2; r^2 = 0.01) because non-glacial lakes were usually smaller and more productive than glacial ones. Moreover, like the smolt production estimates, EV corrected adult production was less variable and produced a more consistent forecast compared to surface area based projections.

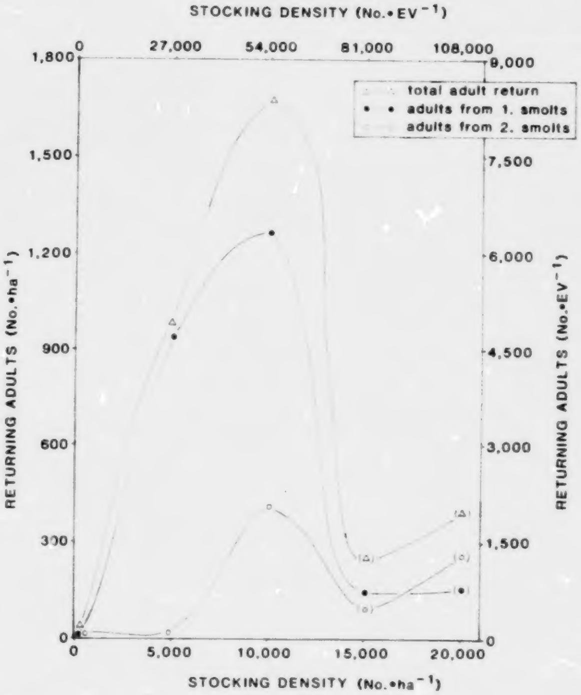

FIG. 10. Numbers of adult sockeye returning and forecast to return to Leisure Lake from fry stocked at increased densities in successive years. Returning adults and stocking densities are expressed in both units of lake surface area (ha) and euphotic volume (EV). Symbols in parentheses show numbers of adults forecast to return using the smolt length versus ocean survival relationship (B) in Fig. 7, and observed numbers and sizes of Leisure Lake smolts.

Overall long-term ASP of large and small, glacial and clear lake systems can be estimated at 2 400–2 500 fish$\bullet$EV^{-1}.

From experimental manipulations of fry densities, we have developed two predictive equations (all terms have been described previously):

1. Log SW = 5.78 − 1.09 log SD (EV); r^2 = 0.99 (Fig. 3)
2. % FWS = 1.89 + 51.86 Log SW; r^2 = 0.92 (Table 2)

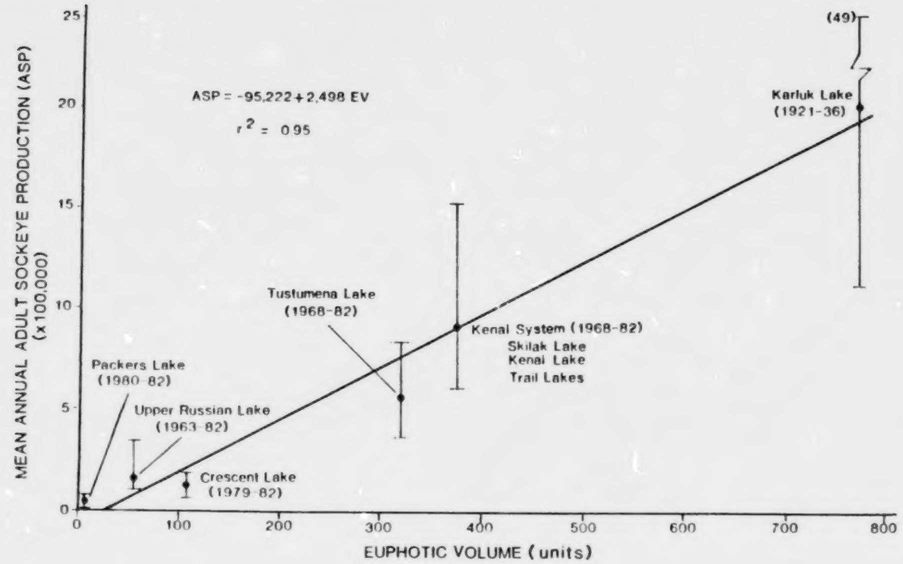

FIG. 11. Empirical relationship between total adult sockeye production (ASP) and the trophogenic zone (units of euphotic volume) for six Alaskan nursery lakes. Points represent either clear, stained or glacial lakes. The years of adult returns, and the range in production estimates over those years are shown by horizontal bars. Euphotic volume (EV) measurements cover non-contiguous years, except for Packers and Crescent lakes, although the comparable EV of Karluk Lake in the 1920's (Juday et al. 1932) and 1980's suggest this to be a source of little error.

Also, from empirical observations on nursery lakes, we have formulated four relationships (all terms have been described previously):

3. $SN = -42\ 021 + 23\ 010\ EV$; $r^2 = 0.97$ (Table 6)
4. $\text{Log}\ SL = 1.71 + 0.31\ \text{Log}\ SW$; $r^2 = 0.99$ (Fig. 1)
5. $\text{Log Ocean Survival} = -2.647 + 0.035\ SL - 0.000142\ (SL)^2$; $r^2 = 0.36$ (Fig. 7)
6. $ASP = -95\ 000 + 2\ 498\ EV$; $r^2 = 0.95$ (Fig. 11)

For nursery lakes capable of supporting density-dependent growth, a stocking density (SD) of ~110,000 fry•EV^{-1} (Fig. 2) would result in forecasting the production of a 1.9 g age 1. smolt (equation 1). This corresponds to a threshold sized smolt of 2 g (Fig. 1) which is then used to estimate a brood-year freshwater survival (FWS) at 18% (equation 2). The original stocking density of 110 000 fry•EV^{-1} multiplied by a survival to smolt of 18% yields a smolt population estimate of 20 000 smolts•EV^{-1}. This is very close to the 23 000 smolts•EV^{-1} found in the empirical relationship derived from rearing limited lakes (equation 3).

The threshold smolt size of 2 g can be converted to an equivalent length (equation 4) of 64 mm which results in a predicted ocean survival of 10% (equation 5). That is, the nearly 20 000 smolts•EV^{-1} of 2 g size produced by an original stocking density of 110 000 fry•EV^{-1} forecast the production of nearly 2 000 adults •EV^{-1}. This is consistent with our empirical observations of rearing limited sockeye systems (equation 6) that produce 2 400–2 500 adults•EV^{-1}. Moreover, the overall ocean survival estimate derived from a comparison of equations 3 and 6 i.e., 2 500 adults •EV^{-1}/23 000 smolts •EV^{-1} equals 11%. Finally, use of a 2 g sized smolt population throughout the calculations (outlined above) becomes the model for systems capable of density-independent rearing. Thus, through validating empirical observations with experimental results, a set of equations emerge that are useful in estimating adult production levels from any stocking density based on a lake's euphotic volume, and the knowledge of density-dependent versus density-independent juvenile rearing.

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Attempts to Re-Establish Sockeye Salmon (*Oncorhynchus nerka*) Populations in the Upper Adams River, British Columbia, 1949–84

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Abstract

WILLIAMS, I. V. 1987. Attempts to re-establish sockeye salmon (*Oncorhynchus nerka*) populations in the Upper Adams River, British Columbia, 1949–84, p. 235–242. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The Upper Adams sockeye population became extinct after a series of blockages prevented the majority of spawners from reaching their natal stream. Attempts to rehabilitate the population have taken place from 1949 to 1985. Egg and fingerling transplants from 1949 to 1975 resulted in very few returns to the river. A sixfold increase in spawners from 1980 to 1984 was attributed to several factors. First, although the original transplants did not produce significant numbers of returning spawners, they probably provided a seed population which was genetically fit for the Upper Adams watershed. Second, short term rearing was included in the 1980 brood program, thus giving the sockeye fry an advantage over natural fry. Third, natural survival of sockeye from much of the Thompson district has increased from 1980 to 1984. Further rehabilitation efforts will be required, including management initiatives if the Upper Adams sockeye are to be returned to their former population levels.

Résumé

WILLIAMS, I. V. 1987. Attempts to re-establish sockeye salmon (*Oncorhynchus nerka*) populations in the Upper Adams River, British Columbia, 1949–84, p. 235–242. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La population de saumon nerka peuplant la partie supérieure de la rivière Adams est disparue après une série d'obstructions qui a empêché la majorité des géniteurs d'atteindre leur ruisseau natal. De 1949 à 1985, on a déployé des efforts de rétablissement de la population. Des déversements d'oeufs et de tacons effectués de 1949 à 1975 n'ont pas entraîné d'importantes remontées dans le cours d'eau. De 1980 à 1984, le nombre de géniteurs a sextuplé. Ceci peut être attribué à plusieurs facteurs. Premièrement, quoique les premiers saumons déversés n'aient pas généré un nombre significatif de géniteurs amontants, ils ont probablement servi de stock reproducteur génétiquement adapté au bassin versant de la partie supérieure de la rivière Adams. De plus, l'élevage à court terme était inclus dans le programme de 1980 relatif au stock géniteur, ce qui a donné un avantage à ces alevins par rapport aux alevins sauvages. Vient s'ajouter ensuite une survie naturelle accrue du saumon nerka dans le district de la Thompson de 1980 à 1984. D'autres efforts de rétablissement seront nécessaires, y compris des initiatives de gestion, afin de ramener la population de saumon nerka peuplant la partie supérieure de la rivière Adams à ses effectifs antérieurs.

Introduction

The Upper Adams sockeye population was probably eliminated by a combination of intense fishing pressure and man-made barriers which prevented the return of spawners. One significant barrier was a splash dam at the upper end of Adams River near the outlet of Adams Lake (Fig. 1). This dam, built about 1907 and relocated in 1908 by a logging company, was used to store water which would be suddenly released to flash-float logs down the river. Although the dam incorporated a small fishway, its operation periodically created dry channels, and violent man-made surges, effectively blocking migration (Thompson 1945).

Railway construction at Hell's Gate in the Fraser River canyon during 1911–12 caused another, and major, barrier. Rock dumped into the river restricted the channel and in 1914 a major rock slide occurred during tunnel construction. The slide was removed by 1915, but resulted in a severely restricted passage area for sockeye salmon when the water levels were between 26 and 40 feet as measured at a gauge below Hell's Gate (Thompson 1945). The timing of the occurrence of these water levels corresponded to the passage of the early sockeye runs which included the Upper Adams run. The restricted passage created at Hell's Gate combined with the continued operation of the Adams River splash dam was catastrophic for the 1913 run. Fisheries overseer Fall's observations, reported by Babcock, Commissioner of Fisheries for B.C., in his 1913 report, were as follows: "...the run of sockeye to Adams Lake in August and September of 1901, 1905 and 1909 was so great that every tributary of the lake extending to Tumtum Lake, at the head of the watershed was crowded with spawning salmon. I visited the headwaters in 1905 and 1909 and saw countless thousands of dead and spawning fish there. An inspection this year showed very few salmon on any of the beds." (Can. Dep. Fish. 1913). The continued decline of the run was probably due to a combination of overfishing (Babcock; B.C. Fish. Dep. Rep. 1919) and limited passage at both Hell's Gate and the Adams River splash dam (Thompson 1945).

The splash dam on the Adams River ceased to operate in 1922 and was removed in 1945. Fishways were completed at Hell's Gate in 1946. While these corrective measures have been chiefly responsible for the success of the famous Adams River sockeye population (a late run which was not as seriously affected by the Hell's Gate blockage), field observations from 1941 and 1950–53 revealed no sockeye spawning in the Upper Adams system. Therefore, with no evidence that an indigenous sockeye population remained in the Upper Adams River, the International Pacific Salmon Fisheries Commission (IPSFC) began a series of transplants of eggs and young in an attempt to restore this valuable summer run.

Materials and Methods

ADAMS LAKE WATERSHED

Adams lake, situated in the South Thompson District of the Fraser River system, is part of the Shuswap Lake watershed. It is oriented in a north-south direction with the Upper Adams River flowing into the north end of the lake and the Adams River flowing from the south end of Adams Lake into the west end of Shuswap Lake (Fig. 1). Adams Lake has a surface area of 138 km^2 and a mean depth of 169 m.

The Upper Adams River, Momich River, and Pass Creek tributaries support sockeye salmon (Fig. 1). The Upper Adams River, approximately 520 km from the mouth of the Fraser River, is the largest, containing an estimated 1.25 million m^2 of spawning ground in the 75 km from the mouth to Tumtum Lake (IPSFC unpublished data). The Momich River drains a series of three small lakes approximately 10 km from the Upper Adams River and is the second largest tributary. Small areas in the $^1/_2$ km of Momich River connecting the first and second lakes at the top end of the watershed, and the first 300 m of Cayenne Creek, a tributary to this section, contain the spawning grounds for sockeye in the Momich system. The third tributary, Pass Creek, is located on the west shore of Adams lake approximately 19 km from the lake outlet. It is very small and has limited spawning grounds. However, sockeye also spawn in the lake near the outlet.

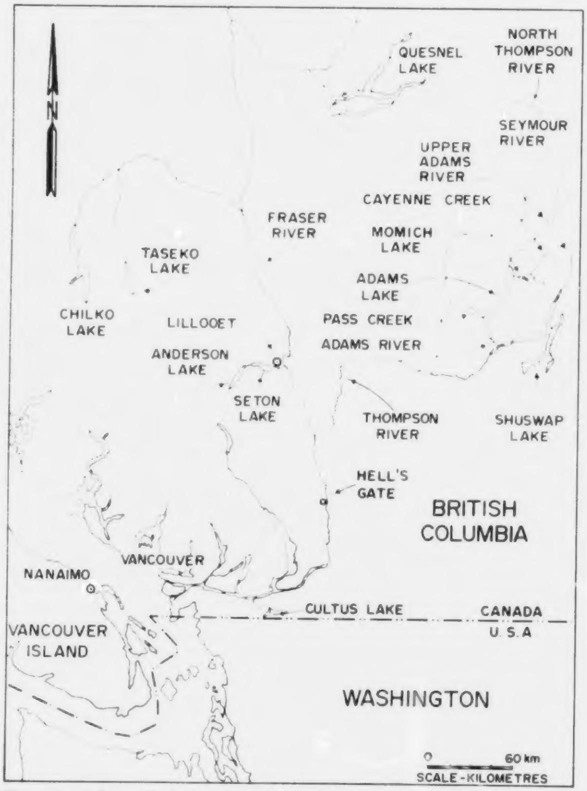

FIG. 1. Adams Lake and other Fraser River tributaries.

ADAMS LAKE SOCKEYE POPULATIONS

The sockeye spawners in the Adams Lake watershed are primarily 4-yr-old fish (age 4_2 by conventional North American nomenclature) and classified into "early" and "late" spawning populations. The Upper Adams and Momich rivers have early runs which spawn between August 27 and September 15. The late runs spawn between October 11 and November 3, occur in all tributaries, and include lake spawners which are considered to be an extension of the large

Adams River run (i.e., they are part of the same stock).

The early spawning populations in the Upper Adams River in the early 1900's were apparently relatively large, although no numerical estimates are available (Can. Dep. Fish. 1913). Field observations from 1950 to the present indicate a very small population, ranging from none to approximately 3 500 (Fig. 2). This is an early run with an estimated timing through Juan de Fuca Strait that is slightly earlier than the prominent Chilko run (Fig. 3). The Early Momich run was first observed in 1960 and has since grown to 5 854 spawners (Table 1).

The late runs to all the tributaries of Adams Lake are small. The first enumeration of the late-run Momich population in 1942 yielded an estimate of 158 spawners. Since then, the population has fluctuated from 58 to 785 spawners on this cycle, with only a few age 3_2 and no age 4_2 sockeye observed in the other cycle years. Pass Creek populations from 1942 to the present have ranged from two fish to 1 448 3-yr-old sockeye in 1957 and a maximum of 2 725 4-yr-olds in 1982. The lake spawning population has been relatively large, exceeding 100 000 spawners in 1942, however, as noted above, this is considered to be an extension of the Adams River run.

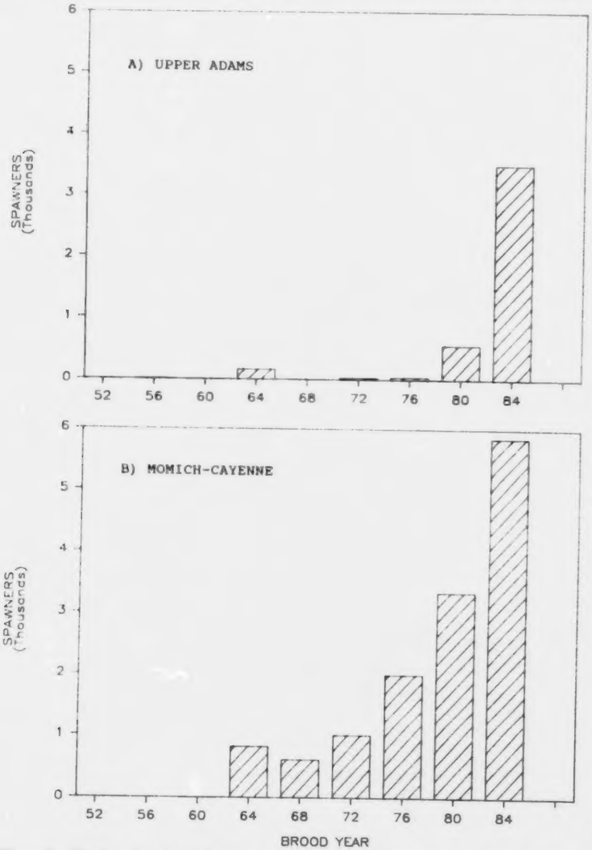

FIG. 2. Early timed sockeye salmon escapements to two tributaries of Adams Lake in the 1912 cycle, 1952–84.

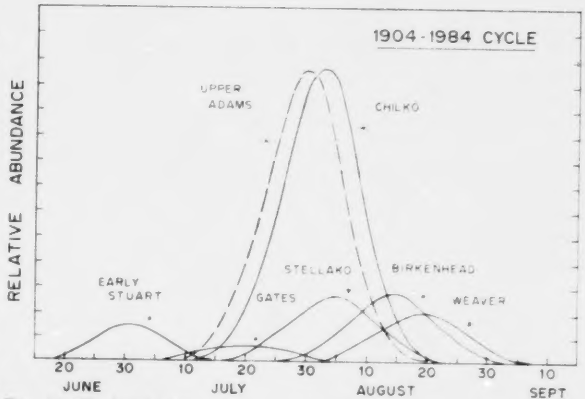

FIG. 3. Timing of the Adams, and some other sockeye runs on the 1904 cycle.

DONOR SOURCES

Two Fraser River tributary populations, originating in the Seymour and Taseko Rivers, were used as donor stocks for transplants to the Upper Adams River from 1949 to 1975. A third stock from Cayenne Creek was used for the 1980 and 1984 transplants. All are summer run stocks with migration timing similar to that of the early Upper Adams population. This river, located in the South Thompson district, drains into Seymour Arm on Shuswap Lake. The "Seymour" sockeye spawn approximately 540 km from the Fraser River mouth. The Taseko River is located in the Chilko district, and its sockeye salmon population spawns approximately 664 km from the mouth of the Fraser. The Taseko is a glacial stream flowing into the south end of Taseko Lake. Cayenne Creek is located approximately 12 km from the Upper Adams River. This small creek with very limited spawning area flows into the Momich River and then into Momich Lake and subsequently into Adams Lake (Fig. 1).

The nursery lakes of the donor and Upper Adams stocks are somewhat different in geography and limnology. Taseko Lake is oriented north–south with smolts exiting north. The lake is a cold, relatively unproductive glacial lake with zooplankton volumes ranging from 0.02 to 0.04 cc/m^3. Seymour Arm in Shuswap Lake is oriented north–south and the main arm is oriented east–west with smolts exiting west. Shuswap is warmer and more productive than Taseko Lake, having annual mean zooplankton volumes as high as 1.1 cc/m^3.

Adams lake is oriented north–south with smolts exiting south. It is slightly colder than Seymour Arm with zooplankton volumes reaching 0.9 cc/m^3.

EGG TAKE AND TRANSPLANT METHODS

From 1949 to 1984, 14 egg transplants, two advanced fry transplants, and two fingerling transplants have taken place. Two methods were used in taking eggs. A standard wet method for egg fertilization was used during 1949–75 (Piper et al. 1982). The eggs were held in a temporary field station near the donor spawning grounds until eyed. Eyed eggs from the 1949–60 egg takes were transported to the Upper Adams site in milk cans filled with water and planted approximately 12 km from the river mouth. There were no transplants from 1961 to 1973.

The 1974 and 1975 eggs were water-hardened and immediately flown to an incubation site adjacent to the Upper Adams spawning grounds. The eggs were incubated to the eyed stage in Heath trays mounted in a mobile hatchery

TABLE 1. Summary of sockeye (4-yr-old) escapements to the Adams Lake watershed 1949–85.

Brood year	Upper Adams		Momich-Cayenne		Pass
	Early	Late	Early	Late	Late
1910 Cycle:					
1950	0		0	158	98
1954	194		0	785	859
1958	291		0	368	402
1962	79		0	217	935
1966	63		0		334
1970	4		0	360	507
1974	13		0		171
1978	N.D.		0	65	547
1982	124		0	112	2 725
1911 Cycle:					
1951	0			0	0
1955	0			0	0
1959	0			0	0
1963	5			0	0
1967	0		0	0	0
1971	0		0	0	2
1975	23		38	0	2
1979	0		0	0	4
1983	0		0		
1912 Cycle:					
1952	0			0	0
1956	9			0	0
1960	2		present	0	0
1964	162		823	0	0
1968	N.D.		617	0	0
1972	31		1 003	0	0
1976	40		1 998		
1980	560		3 345		
1984	3 502		5 854		
1913 Cycle:					
1949					
1953	0				1
1957	0	5			15
1961	0		0	0	0
1965	0		0	0	0
1969	0		0	0	8
1973	0		0	0	0
1977	0		11		
1981	0		63		
1985	83		56		

* Blank space indicates no observation.

(trailer) and planted in a location similar to the previous plants.

Eggs from the 1980 brood were handled in a similar way. However, water-hardened eggs were flown to the Cultus Lake Laboratory at Sweltzer Creek, incubated in Heath trays to the advanced alevin stage, then flown back to Adams Lake for rearing.

The 1984 transplant involved crossing females from Cayenne Creek with males from Upper Adams. Eggs were stripped into dry containers and transported by truck from Cayenne Creek to a site adjacent to the Upper Adams River, 10 km below the spawning grounds. Upper Adams males were netted from the spawning grounds, and trucked to net pens at the incubation site. The eggs were fertilized using a standard wet method, water-hardened and incubated to the eyed stage in Heath trays in the trailer facility. A small group of Upper Adams eggs, fertilized with Upper Adams males, were handled in the same way.

The Cayenne and Upper Adams eggs were then divided into two groups. One group was planted in a prepared gravel bed in the Upper Adams River. For this, a small area of gravel was removed from the river bed approximately 100 m upstream of the incubation site and replaced with washed gravel pieces ranging in diameter from ³/₄″ to 3″. When the planting in the prepared bed was complete three wire baskets each containing 100 eggs in 0.02 m^3 of gravel were buried near the upstream edge of the gravel bed and another three were buried at the downstream end. Two were removed at the alevin stage, two at and advanced alevin stage, and two at the fry stage to permit a check on survival. The second group was planted in an upwelling gravel incubation box similar to ones used at Babine Lake (Ginetz 1976). The box was buried in the river bank adjacent to the prepared gravel bed and below the frost level. Traps were installed to capture the hybrid fry as they emerged from the box.

REARING

Progeny from the 1949 and 1952 brood egg takes were reared at the IPSFC Horsefly Field Station, located on Horsefly Lake, B.C., and released into Adams Lake.

Fry of the 1980 brood (Cayenne Creek stock) were reared in four polyethylene cones similar to some used in Alaska (Heard and Martins 1979). The cones were attached to a barge anchored near the mouth of the Upper Adams River. Earliest emerging fry (334 000) were placed in cones labelled A and B; later fry (393 000) were reared in cones C and D. The fry were fed freeze-dried calanoid copepods for 24–40 days, depending on time from emergence to release. The barge was then towed to a site several kilometres down Adams Lake where the fry were released during the night.

Fry of the 1984 brood were captured as they exited from the incubation box and placed in rearing troughs installed at the incubation site. They were fed freeze-dried plankton for 28 days and released directly to the Upper Adams River. Growth was monitored during the rearing periods in 1981 and 1985. Samples of fish were taken weekly from each trough (84 brood) or cone (80 brood) and preserved in 10% formalin. Lengths and wet weights were determined in the field and dry weights were determined at the Cultus Lake Laboratory. Fry from the river plant were not used for rearing.

ENUMERATIONS

Sockeye spawners in the Adams Lake watershed have been enumerated by the IPSFC using a combination of live and dead counts. The population is estimated by multiplying the sum of the highest number of live sockeye observed during the season plus the number of dead to that date, by 1.8. This calculation was developed by the IPSFC on the basis of numbers generated in a standard tag recapture enumeration and compared with a live count of the same population (Woodey 1984). The first IPSFC enumeration of the early Upper Adams population was in 1941. (There were no observations from 1942 to 1949). After 1949 enumerations were done annually between August 20 and October 9. The cycle years following transplants received 2–6 visits, each lasting as long as 5 days. In other years, the number of visits has ranged from one to three, each lasting 1 day.

Results

TRANSPLANTS AND SPAWNER RETURNS

1) *Egg Plants* — There were 14 transplants totalling 10.37 million eyed eggs to the Upper Adams River from 1949 to 1984. Of these a total of 7.77 million Seymour eggs were used as donor stock in 10 plants from 1949 to 1975. These plants ranged in size from 158 000 to 2.14 million eggs (Table 2). The Taseko population was used as a donor stock for another three transplants in 1958, 1959, and 1960, totalling 2 152 000 eggs. None of these Seymour or Taseko plants resulted in significant returns to the Upper Adams spawning ground on the following cycle year (Table 2). The 1911 cycle produced a total of 28 adults from a total of 4.4 million eggs. No spawning or dead sockeye were observed in four live counts in 1979 (the cycle year following the largest plant of 2.14 million) or in 1983.

The best returns have been on the 1910 and the 1912 cycles. The best rate of return to the river (excluding any catch) was 0.029% of the 667 000 Seymour eggs planted in 1950 in the 1910 cycle. This cycle also had the largest spawner return (291 in 1958) following a transplant, however, the contribution from the transplant, if any, cannot be determined as there were also 194 feral spawners in 1954. Since 1958, the estimated spawning population has ranged from 0 (no fish detected) to 124 in 1982. There have been no transplants since 1974 (Table 2). The only check on egg survival on any of the transplants up to 1980 was carried out in 1958 when several plants were excavated and survival was reported as excellent (IPSFC Annual Report 1958).

There have been three egg transplants to the Upper Adams River in years of the 1912 Cycle. A plant of 253 000 eggs was made in 1956 but no salmon were observed in 1960, the cycle year of return. The return of 162 spawners in 1964, followed the plant of 702 000 Taseko eggs in 1960. This was the third largest return of spawners following a transplant. There were no further introductions until 1980, however, during this period the spawning population estimates ranged from 0 (none detected) in 1968 to 560 in 1980 (Table 1). Results from the 400 000 hybrid eggs (Cayenne × Upper Adams) and 48 000 pure Upper Adams eggs in 1984 will not be known until 1988. However, retrieval of egg baskets from the former indicated that survival to alevin was about 98% and survival to fry was 90%.

2) *Fry and Fingerling Plants* — There were two plants of Seymour fingerlings to the Upper Adams River, 84 000 from the 1949 brood and 187 000 from the 1952 brood. The fingerlings were released at the head end of Adams Lake in November of 1950 and 1953. These plants produced virtually no returns on the following cycle years. There were no fish observed in 1953 and the total population was estimated to be only nine spawners in 1956.

The two plants of fry from the 1980 Cayenne brood stock to the Upper Adams system totalled 727 000. The advanced fry held in ponds A and B attained an average length of 26.0 mm when 100% of their yolk was absorbed, and grew very little over the next 13 days (Fig. 4). At release they averaged 26.3 mm fork length, 0.14 g wet wt, and 22.0 mg dry wt (Table 3). Mortality from alevin stage to time of release was 15.8% with a mortality of 2.6% on the final day prior to release. The later emerging fry held in ponds C and D were growing well when released (Fig. 4). The average length of these fry was 27.5 mm and the average wet and dry weights were 0.18 g and 26.1 mg, respectively (Table 3). Total mortality was 8.2% and the final day's mortality was less than 0.1 at release (Williams 1984).

In 1984, the cycle year following this plant, 3 502 spawners returned to the Upper Adams. This is 0.6% of the

TABLE 2. Summary of egg transplants to the Upper Adams River from other watersheds, and spawner returns.

Brood year	Feral spawners	Seymour eggs	Taseko eggs	Total eggs	Spawner return	Percent return
1910 Cycle:						
1950	0	667 000		667 000	194	0.03
1954	194	495 000		495 000	291	0.06
1958	291	483 000	850 000	1 333 000	79	0.01
1974	13	1 374 000		1 374 000	0[a]	0.00
Total	498	3 019 000	850 000	3 869 000	564	0.01
1911 Cycle:						
1955	0	780 000		780 000	0	0.00
1959	0	900 000	600 000	1 500 000	5	0.00
1975	23	2 140 000		2 140 000	0[b]	0.00
Total	23	3 820 000	600 000	4 420 000	5	0.00
1912 Cycle:						
1956	9	253 000		253 000	0	0.00
1960	2		702 000	702 000	162	0.02
Total	11	253 000	702 000	955 000	162	0.02
1913 Cycle:						
1949	0	158 000		158 000	0	0.00
1957	0	520 000		520 000	0	0.00
Total	0	678 000		678 000	0	0.00

[a] 124 spawners in 1982.

[b] No spawners in 1983.

total fry (transplanted and feral stocks) produced, based on an expectation that the 560 feral spawners would produce between 100 000 and 250 000 fry (Table 4). However, it is not possible to determine the relative contributions of transplanted and feral fry, as no marking was done and commercial exploitation rates on these fish are not known. All of the 1984 early run spawning populations in the Thompson District increased significantly over the previous cycle (Table 5). However, the enumeration data indicate a larger return per spawner for the Upper Adams than for the early runs in the Thompson District, including the Momich and similar timed runs in the North Thompson system. These data suggest that the 1980 brood fry did contribute to the 1984 Upper Adams run.

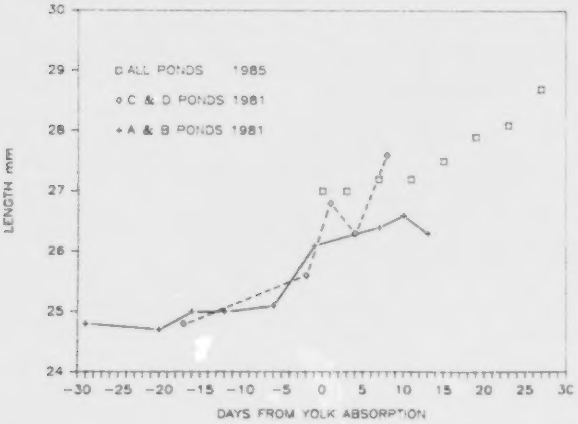

FIG. 4. Lengths of sockeye fry reared at Upper Adams River in 1981 and 1985.

The second fry plant used eggs from the 1984 brood Cayenne females crossed with Upper Adams males. A total of 360 000 fry from the incubation box were released to the Upper Adams River and 33 000 were released to Adams Lake. Sixty thousand were released to the Upper Adams River upon emergence, and 300 000 were released to the river after 28 days of rearing. These latter fish were growing well and averaged 0.24 g and 28.7 mm when released (Fig. 4). The dry weights increased 83% from 20 to 37 mg at release. This is considerably larger than that of the 1980 fry at release.

Discussion

The restoration of a salmon population which has been eliminated must begin through either straying or a transplant. Unfortunately, with few exceptions Fraser River system transplants have met with little measurable success. Transplants within the Fraser River system began in 1884 and were closely coordinated with a large scale sockeye hatchery program. Approximately 84.3 million eggs and 393.5 million fry were transplanted during the period 1884–1934. Within the Shuswap system 16.9 million fry were transplanted to Tappen Creek during 1902–07. The Eagle River received 26.8 million eggs during 1921–31, with the 1928 transplant exceeding 15 million eggs (Aro 1979). The transplant and hatchery program had limited success and in 1936 the Minister of Fisheries recommended closure. Kemerick (1945) indicated similar results with many of the sockeye transplants in Washington State and an analysis by Salmenkova et al. (1983) of chum salmon transplants in the Soviet Union indicated good egg to fry survival but poor returns.

However, there is a recent example of a successful transplant of sockeye. A series of transplants over a 20-yr

TABLE 3. Length and weight of Cayenne Creek sockeye released to Adams Lake, June 2, 1981.

Pond	*n*	Length (mm)	SD	Wet weight (g)	SD	Dry weight (mg)	SD
A	62	26.1	1.1	0.14	0.04	21.5	7.1
B	66	26.5	0.9	0.14	0.03	22.4	5.2
A&B	128	26.3	1.0	0.14	0.04	22.0	6.2
C	64	27.4	1.4	0.17	0.03	25.7	6.0
D	82	27.6	1.4	0.19	0.04	26.4	6.2
C&D	146	27.5	1.4	0.18	0.03	26.1	6.1

TABLE 4. Summary of fry and fingerling transplants to the Upper Adams River and spawner returns.

Brood year	Feral spawners	Cayenne fry	Seymour fingerling	Spawner return	Percent return
1912 Cycle:					
1952	0		187 000	9	0.00
1980	560	334 000		3 502	0.60
1984	3 502	393 000[a]		N.A.	N.A.
1913 Cycle:					
1949			84 000	0	0.00

[a] Hybrid fry: Adams males × Cayenne females.

TABLE 5. Early sockeye escapements to the Thompson district, 1980–84.

Population	Escapement 1980	Escapement 1984	Return/Spawner[a]
Adams Lake:			
Upper Adams	560	3 502	6.25
Momich	3 345	5 854	1.75
North Thompson:			
Raft	5 418	19 098	3.52
Fennel	8 437	11 021	1.31
Seymour	8 309	17 172	2.07

[a] No catch data.

period from 1951 to 1971 plus commercial fishing closures (to protect pink salmon) have resulted in the Frazer Lake run in Alaska growing from nil to 142 000 spawners in 1978 (Blackett 1979). The 1985 escapement is estimated at 485 835, the largest to date. In addition an estimated 165 000 Frazer sockeye were captured in the fishery (Blackett, pers. comm.). This suggests that repeated egg, fry, and adult plants can culminate in successful sockeye salmon runs.

The 1912 cycle Upper Adams run, after two egg transplants, and one fry and one fingerling transplant, is beginning to show some results. While there were no significant returns to the Upper Adams River on the cycle years following the egg or fingerling transplants, an early run did develop in the Momich–Cayenne system. Historically, there has been a small late run in the Momich system on the 1910 cycle, however, the early run in the 1912 cycle was first reported in 1960 (Table 1). This run has grown to 5 854 spawners, probably the maximum considering the limited spawning area (Fig. 2). An examination of escapement, length frequency and scale data from the other early runs in the Thompson District did not reveal any evidence that straying contributed to these populations. However, the proximity of the Momich River to the Upper Adams River and the fact that the fingerlings were released to Adams Lake and not to the Upper Adams River suggests that straying could have established the early Momich run. The work of Bams (1976) also supports the straying theory. Transplant experiments using pink salmon indicated that while the survival of pure donor (non-native) and hybrid (non-native/native) stocks was similar, hybrid pinks were ten times more successful in homing to the natal stream.

The importance of the Momich run is not in its potential production, but in its value as a source of gametes for transplanting to the Upper Adams River. The return of 3 502 to the Upper Adams in 1984 is the first indication that the transplants may be successful. Whether this return was totally from the feral spawners or included a contribution from the fry transplant is open for debate as the fry were not marked. However, the return (to the spawning grounds) per spawner (r/s) of 6.3 for the Upper Adams supports the suggestion that transplanted fry contributed. This r/s is considerably higher than the Momich r/s of 1.8, and the r/s of 2.3 (range 1.3–3.5) for the other similarly timed early runs in the Thompson District (Table 5).

There are several reasons for believing that the transplanted fry contributed to the higher r/s. First, the release of 334 000 fry is estimated to be 1.5 times the number of natural fry produced from the 360 feral females based on a fecundity of 3 300 and an optimistic egg to fry survival of 20%. Approximately 104 000 of the transplant fry were not feeding as voraciously and grew poorly after yolk absorption. Data from feeding trials at Cultus Lake using the same diet as on the Upper Adams indicated that this diet was deficient. It resulted in a very poor growth rate and poor health, however, when the fry were fed a suitable diet the fish recovered quickly (Williams 1984). The remaining 230 000 fry released eight days after yolk absorption, were still growing and seemed in good health when released. Therefore, the addition of fry reared for a short-term more than doubled the feral fry population.

Second, the transplanted fry were introduced to Upper Adams River water as alevins, and subsequently reared for a minimum of 24 days, therefore, they would have imprinted on Adams River water. Third, the 24 days of rearing and release offshore at night should have assisted in predator avoidance. Fourth, the release of fry at the beginning of June was timed with reasonable plankton levels which would provide good feed for sockeye in Adams Lake. Therefore, there is reason to believe that the fry rearing program did contribute to the 1984 return, however, future programs should also incorporate a tagging program.

If success is measured by commercially significant numbers of returning adults, then these transplants were not effective. However, if success is measured by the creation of even a small population, adapted to the Adams Lake watershed environment and capable of providing seed for further expansion, then these transplants were successful. The seemingly unsuccessful transplant attempts in early years may have been important in establishing a genetic base from which survivals can be enhanced using current biological and management technologies. A continued enhancement effort utilizing transplants, egg incubation technology, and improved short term rearing technology could result in a commercially viable run, similar to the Frazer Lake success reported by Blackett (1979).

Acknowledgements

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Prevalence of Visceral Adhesions in Sockeye Salmon (*Oncorhynchus nerka*) in the North Pacific Ocean and Bering Sea

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Abstract

NAGASAWA, K. 1987. Prevalence of visceral adhesions in sockeye salmon (*Oncorhynchus nerka*) in the North Pacific Ocean and Bering Sea, p. 243–253. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The occurrence of visceral adhesions in sockeye salmon was recorded during Pacific salmon surveys in the central North Pacific in 1981–83 and in the western and central North Pacific, the Gulf of Alaska, and the Bering Sea in 1984. The annual prevalence of visceral adhesions ranged from 4.0 to 7.7%. Adhesions occurred most often in the 35–54 cm length groups, but were never found in fish below 30 cm or in those over 65 cm long. Prevalence was at a maximum in age .2 fish but decreased in ages .3 and .4 fish. The proportion of affected salmon increased with increasing duration of freshwater residence of juveniles. Male fish were more often affected than female fish. Visceral adhesions occurred most frequently in immature fish and prevalence fell rapidly with fish maturation. Sockeye salmon with adhesions were widely distributed in the North Pacific Ocean and Bering Sea. Highest prevalences were centered in the western and central North Pacific Ocean between 40° and 48°N from 160°E to 175°W in April–May and in the Bering Sea in June–August. The findings are discussed in relation to the life history of a dracunculoid nematode, *Philonema oncorhynchi*, and the effects of visceral adhesions on sockeye salmon.

Résumé

NAGASAWA, K. 1987. Prevalence of visceral adhesions in sockeye salmon (*Oncorhynchus nerka*) in the North Pacific Ocean and Bering Sea, p. 243–253. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La fréquence des adhérences viscérales chez le saumon nerka a été notée au cours de relevés du saumon du Pacifique effectués dans le centre du Pacifique Nord, de 1981 à 1983, ainsi que dans les parties ouest et centre du Pacifique Nord, le golfe de l'Alaska et la mer de Béring en 1984. Le taux annuel de prévalence des adhérences variait de 4.0 % × 7.7 %. Les adhérences étaient le plus souvent notées chez les poissons du groupe de longueur des 35 à 54 cm et étaient toujours absentes chez les poissons de moins de 30 cm ou de plus de 65 cm de longueur. La prévalence était maximale chez les poissons d'âge .2 et moins importante chez ceux d'âge .3 et .4. La proportion de saumons touchés augmentait avec la durée de séjour en eau douce des juvéniles. Les mâles étaient plus souvent affectés que les femelles. Les adhérences viscérales étaient les plus fréquentes chez les poissons immatures et la prévalence déclinait rapidement avec le degré de maturation. Les saumons nerkas affectés se retrouvaient dans une grande zone du Pacifique Nord et de la mer de Béring. Les valeurs de prévalence les plus élevées étaient concentrées dans l'ouest et le centre du Pacifique Nord, entre 40° et 48°N et 160°E et 175°O en avril et mai, et dans la mer de Bering de juin à août. L'auteur traite de ces résultats dans le contexte de cycle vital du nématode dracunculoïde (*Philonema oncorhynchi*) et des effets des adhérences viscérales chez le saumon nerka.

Introduction

Wild fish populations are affected with parasitic infections and diseases, but the impact of these afflictions on the populations is poorly understood. Multiple mesenteric and peritoneal adhesions in high-seas Pacific salmon were first reported by French (1965), who stated that they were observed most frequently in sockeye salmon (*Oncorhynchus nerka*) and rarely in chum salmon (*O. keta*). This pathological condition is caused by *Philonema oncorhynchi*, a nematode parasite of the body cavity of salmonids. Platzer and Adams (1967) reported that sockeye salmon infected with this parasite developed visceral adhesions in the laboratory when the larvae moved from the tissues to the body cavity of fish. Margolis (1970) mentioned that visceral adhesions are the result of a host reaction associated with the migration of the parasite. However, there is still little information concerning visceral adhesions in sockeye. More information on the occurrence, distribution, and severity of this disease is necessary to assess the effects on sockeye salmon at the population level.

As a member of the International North Pacific Fisheries Commission (INPFC), Japan has conducted research on high-seas salmonids in the North Pacific Ocean and Bering Sea on board research vessels and motherships. When I was aboard the research vessel *Hokushin maru* during the period 1981–83, I recorded the presence of visceral adhesions in sockeye salmon in order to (1) determine the frequency of occurrence of fish with adhesions by year and area; (2) collect biological data relative to the visceral adhesions; and (3) elucidate the effects on sockeye salmon. However, the survey areas were restricted to the central North Pacific Ocean. A comprehensive survey was needed to determine the ocean distribution of affected salmon throughout the North Pacific region and obtain more biological information about them. Fortunately, scientists on board seven Japanese salmon research vessels collected, at my request, data on the occurrence of visceral adhesions in sockeye in a wide area of the North Pacific Ocean and Bering Sea in 1984.

This paper presents information on the prevalence of visceral adhesions in high-seas sockeye salmon derived from such shipboard research surveys during 1981–84. Because the results obtained in 1981–83 have been reported in detail elsewhere (Nagasawa 1985), the data during this 3-year period, excluding annual prevalence data, are combined in this paper.

Materials and Methods

SURVEY AREAS AND PERIODS

A total of 17 285 sockeye salmon were collected from 261 locations in the North Pacific Ocean and Bering Sea during the springs and summers of 1981–84: 1 700 fish in July 1981, 1 086 fish in May and June 1982, 1 149 fish in May and June 1983, and 13 350 fish in April to August 1984. The survey areas during the first 3 years were the central North Pacific Ocean (41°–52°N, 167°E–177°W), but the 1984 survey areas were greatly expanded to include the western and central North Pacific (35°–53°N, 144°E–168°W), the Gulf of Alaska (37°–55°N, 154°–156°W), and the central part of the Bering Sea (54°–61°N, 174°E–175°W). The survey period in 1984 was divided into two seasons (April–May and June–August) because most research vessels made two cruises according to these seasons. Fish were collected by one vessel (*Hokushin maru*) during 1981–83, and by seven vessels (*Hokushin maru*, *Iwaki maru*, *Wakatake maru*, *Hokuho maru*, *Riasu maru No. 2*, *Hokusei maru*, and *Oshoro maru*) in 1984. Surface gillnets with mesh sizes varying from 48 to 157 mm, and longlines were used as fishing gear.

EXAMINATION OF SOCKEYE SALMON

On removal from gillnets, fish were processed by recording fork length, body weight, sex, gonad weight, and the presence or absence of visceral adhesions. Since longline gear was used to catch salmon for tagging, only fish that were not tagged were examined and similar biological data were collected. A scale for age determination was removed from the standard INPFC-preferred area (Major et al. 1972) of the body of each fish.

AGE DETERMINATION OF SOCKEYE SALMON

Scales were read by the staff of the Far Seas Fisheries Research Laboratory, Shimizu, Japan. Ages of fish were recorded according to the European formula (Koo 1962): the first numeral is freshwater age, and represents the number of winters spent in fresh water after hatching, and the second numeral is ocean age, and shows the number of winters spent at sea.

MATURITY DETERMINATION OF SOCKEYE SALMON

Maturity of sockeye salmon was determined by the gonad

TABLE 1. Criteria of gonad weight (grams) for determining maturity stages of sockeye salmon caught on the high seas in the North Pacific Ocean and Bering Sea.[a]

Sex	Maturity stage	Season								
		~mid-May	late May	early June	mid-June	late June	early July	mid-July	late July	early August
Female	Immature	≤9	≤14	≤14	≤19	≤19	≤24	≤24	≤24	≤24
	Maturing I	10–50	15–50	15–50	20–50	20–50	25–50	25–50	25–50	25–50
	Maturing II	…	…	…	…	51–100	…	…	…	…
	Maturing III	…	…	…	…	≥101	…	…	…	…
Male	Immature	≤1	≤1	≤1	≤2	≤2	≤2	≤4	≤4	≤4
	Maturing I	2–20	2–20	2–20	3–20	3–20	3–20	5–20	5–20	5–20
	Maturing II	…	…	…	…	21–50	…	…	…	…
	Maturing III	…	…	…	…	≥51	…	…	…	…

[a] The criteria were primarily established by Takagi (1961) and developed by Osako (1973) and the staff of the Far Seas Fisheries Research Laboratory, Shimizu, Japan.

weight criterion (Table 1) and assigned to one of four stages: immature, maturing I, maturing II, and maturing III. Throughout the text, immature fish refer to those fish that would have remained at sea one or more winters if they had not been caught, and maturing fish are those that were destined to spawn in the year of capture.

OCEAN DISTRIBUTION

The ocean distribution of sockeye with visceral adhesions in the North Pacific Ocean and Bering Sea was analysed by season and by INPFC statistical area (5° of longitude and 2° of latitude). Area E7048, for example, represents a rectangle bounded by 170°–175°E and 48°–50°N.

DEFINITIONS

The terms prevalence and mean intensity are used in accordance with the definitions provided by Margolis et al. (1982). In the present paper prevalence refers to the ratio, expressed as a percentage, of the number of fish with visceral adhesions to the total number examined, or to the percentage of fish in a sample infected with *P. oncorhynchi*. Mean intensity of infection is the mean number of *P. oncorhynchi* among the infected group in a sample of fish.

Results

Twelve hundred and thirty-three of 17 285 (7.1%) sockeye salmon examined during 1981–84 were affected with visceral adhesions (Table 2). The annual prevalence of this disease ranged from 4.0% in 1982 to 7.7% in 1984. Sockeye with adhesions were captured at 201 of 261 (77.0%) locations.

TABLE 2. Prevalence of visceral adhesions in sockeye salmon caught in the North Pacific Ocean and Bering Sea, 1981–84.[a]

Year	Male	Female	Total
1981	58/883 (6.6)[b]	26/817 (3.2)	84/1 700 (4.9)
1982	32/545 (5.9)	11/541 (2.0)	43/1 086 (4.0)
1983	69/764 (9.0)	10/385 (2.6)	79/1 149 (6.9)
1984	665/7 263 (9.2)	359/6 071 (5.9)	1 027/13 350 (7.7)[c]
Total	824/9 455 (8.7)	406/7 814 (5.2)	1 233/17 285 (7.1)

[a] The prevalence data from 1981 to 1983 were taken from Nagasawa (1985).

[b] Number with adhesions/number examined (percentage).

[c] Sixteen unsexed fish, of which three had adhesions, are included.

EFFECT OF FISH SEX ON PREVALENCE

Visceral adhesions occurred more frequently in males than in females (Table 2). This relationship pertained in all 4 years from 1981 to 1984 and higher prevalences in males were observed at 146 of 201 (72.6%) locations.

RELATIONSHIP BETWEEN FISH SIZE AND PREVALENCE

The occurrence of visceral adhesions was closely related to fish size. Adhesions were most commonly found in fish 35–54 cm in length (Fig. 1). Although no adhesions were detected in fish less than 30 cm long, the percentage of affected salmon increased in fish from 30 to 34 cm in length and reached a maximum in fish 40–44 cm in length. However, the prevalence decreased in fish greater than 45–49 cm in length and adhesions were absent in fish over 65 cm.

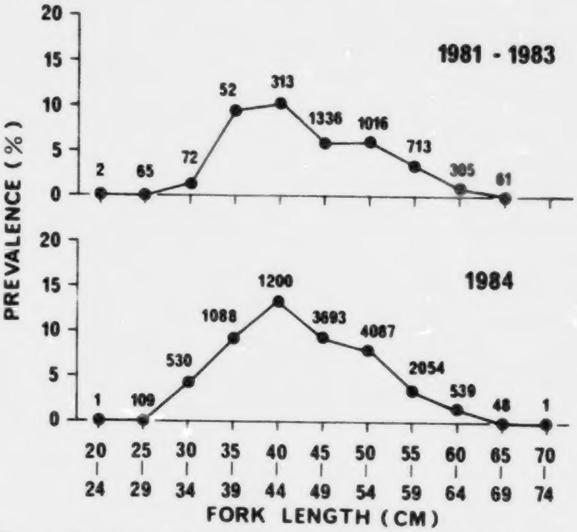


FIG. 1. Prevalence of visceral adhesions in sockeye salmon of different length groups caught in the North Pacific Ocean, 1981–83 (*top*) and in the North Pacific Ocean and Bering Sea, 1984 (*bottom*). Numerals refer to the number of fish examined.

Between the spring (April–May) and summer (June–August) of 1984, there was a marked difference in the relationship of fish size and prevalence (Fig. 2). In the former season, prevalences in the 35–49 cm length groups were high (13.6–21.5%), but they decreased to 6.7–8.5% in the latter season.

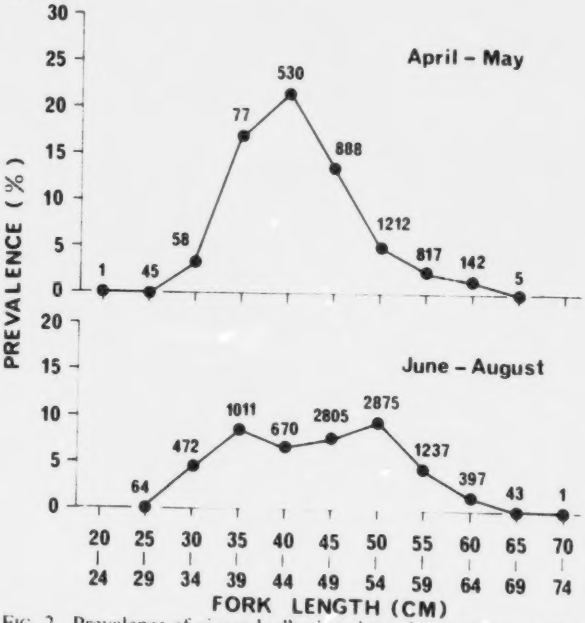


FIG. 2. Prevalence of visceral adhesions in sockeye salmon of different length groups caught in the North Pacific Ocean and Bering Sea in April-May (*top*) and June-August 1984 (*bottom*). Numerals refer to the number of fish examined.

EFFECT OF FISH MATURITY ON PREVALENCE

Visceral adhesions occurred most often in immature fish, and there was a sharp decrease in prevalence with increasing maturation of fish: 9.1% in immature fish (n = 10 602 for 1981–84), 5.4% in maturing-I fish (4 167), 1.3% in maturing-II fish (1 749) and 0.2% in maturing-III fish (533). This decrease in prevalence was similar for both sexes of fish, although prevalence levels in females were consistently lower than those in males (Fig. 3).

In immature fish, great seasonal changes in prevalence were observed in 1984. Spring to summer declines were 17.7 to 9.2% in males and 14.6 to 7.3% in females.

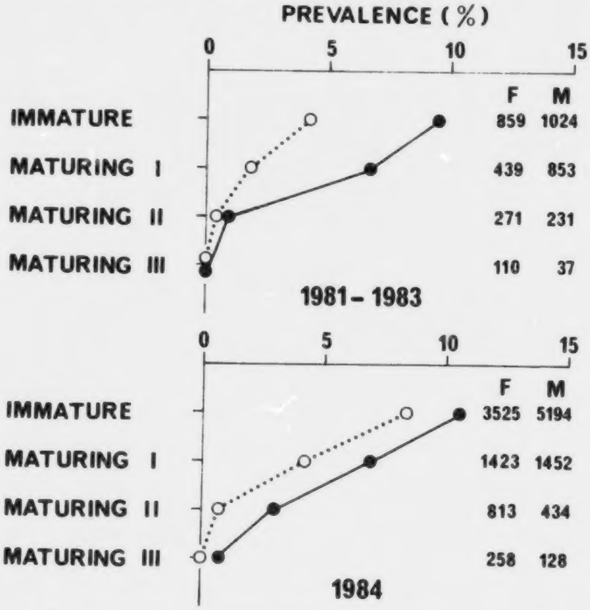


FIG. 3. Prevalence of visceral adhesions in sockeye salmon of different maturity stages caught in the North Pacific Ocean, 1981–83 (*top*) and in the North Pacific Ocean and Bering Sea, 1984 (*bottom*). Numerals refer to the number of each sex. F (○), females; M (●), males.

RELATIONSHIP OF FISH AGE WITH PREVALENCE

Of the 15 age-groups recognized during this study, age 3.2 sockeye were the most frequently affected, followed by fish of ages 2.2 and 2.1 (Table 3).

No adhesions were found in fish of freshwater age 0, but there was a steady increase in prevalence with increasing length of freshwater residence (Table 4). Prevalence levels were also influenced by the length of the sockeye's ocean life. Fish of ocean age 2 were most often affected with visceral adhesions, but fish of other ocean ages, especially those of ages .3 and .4, had low prevalences (Table 5).

TABLE 3. Prevalence of visceral adhesions in sockeye salmon of different age groups caught in the North Pacific Ocean and Bering Sea, 1981–84.

Age group	1981–83	1984	Total
0.1	0/1 (0)[a]	0/3 (0)	0/4 (0)
1.1	1/63 (1.6)	15/581 (2.6)	16/644 (2.5)
2.1	1/61 (1.6)	92/952 (9.7)	93/1013 (9.2)
3.1	0/9 (0)	2/17 (11.8)	2/26 (7.7)
X.1[b]	0/11 (0)	6/105 (5.7)	6/116 (5.2)
0.2	0/6 (0)	0/12 (0)	0/18 (0)
1.2	79/1471 (5.4)	282/3527 (8.0)	361/4998 (7.2)
2.2	77/889 (8.7)	385/3384(11.4)	462/4273 (10.8)
3.2	8/54 (14.8)	28/179 (15.6)	36/233 (15.5)
X.2	12/135 (8.9)	48/586 (8.2)	60/721 (8.3)
0.3	0/18 (0)	0/14 (0)	0/32 (0)
1.3	4/507 (0.8)	40/1314 (3.0)	44/1821 (2.4)
2.3	5/368 (1.4)	49/1326 (3.7)	54/1694 (3.2)
3.3	2/28 (7.1)	7/132 (5.3)	9/160 (5.6)
X.3	1/61 (1.6)	7/216 (3.2)	8/277 (2.9)
0.4	0/1 (0)	0/1 (0)	0/2 (0)
1.4	0/17 (0)	1/50 (2.0)	1/67 (1.5)
2.4	0/4 (0)	0/16 (0)	0/20 (0)
X.4	0/1 (0)	0/1 (0)	0/2 (0)

[a] Number with adhesions/number examined (percentage).

[b] Undetermined age is expressed by X.

TABLE 4. Prevalence of visceral adhesions in sockeye salmon of different freshwater ages caught in the North Pacific Ocean and Bering Sea, 1981–84.

Fresh-water age	1981–83	1984	Total
0.	0/26 (0)[a]	0/31 (0)	0/57 (0)
1.	84/2058 (4.1)	338/5472 (6.2)	422/7530 (5.6)
2.	83/1322 (6.3)	526/5678 (9.3)	609/7000 (8.7)
3.	10/91 (11.0)	37/328 (11.8)	47/419 (11.2)

[a] Number with adhesions/number examined (percentage).

TABLE 5. Prevalence of visceral adhesions in sockeye salmon of different ocean ages caught in the North Pacific Ocean and Bering Sea, 1981–84.

Ocean age	1981–83	1984	Total
.1	2/145 (1.4)[a]	115/1658 (6.9)	117/1803 (6.5)
.2	176/2555 (6.9)	743/7688 (9.7)	919/10243 (9.0)
.3	12/982 (1.2)	103/3002 (3.4)	115/3984 (2.9)
.4	0/23 (0)	1/68 (1.5)	1/91 (1.1)

[a] Number with adhesions/number examined (percentage).

OCEAN DISTRIBUTION

To illustrate the ocean distribution of sockeye salmon with visceral adhesions, data from the 1984 survey were used because they provided the broadest coverage of the North Pacific Ocean and Bering Sea (Fig. 4). Figure 5 shows the distribution of percentage prevalences of visceral adhesions by 2° × 5° INPFC statistical areas, and Fig. 6 and 7 show the size and maturity compositions, respectively, of sockeye by INPFC areas.

In the spring months (April–May), the southern limit of the distribution of sockeye salmon was about 42°N. Although surveys in the Bering Sea and the Gulf of Alaska were not conducted during this period, the most notable feature was the concentration of affected salmon in INPFC areas E6540 (prev. = 29.4%), E7042 (25.0%), E7542 (22.8%), 8044 (28.8%), and 8046 (24.5%). Fish caught in these areas were

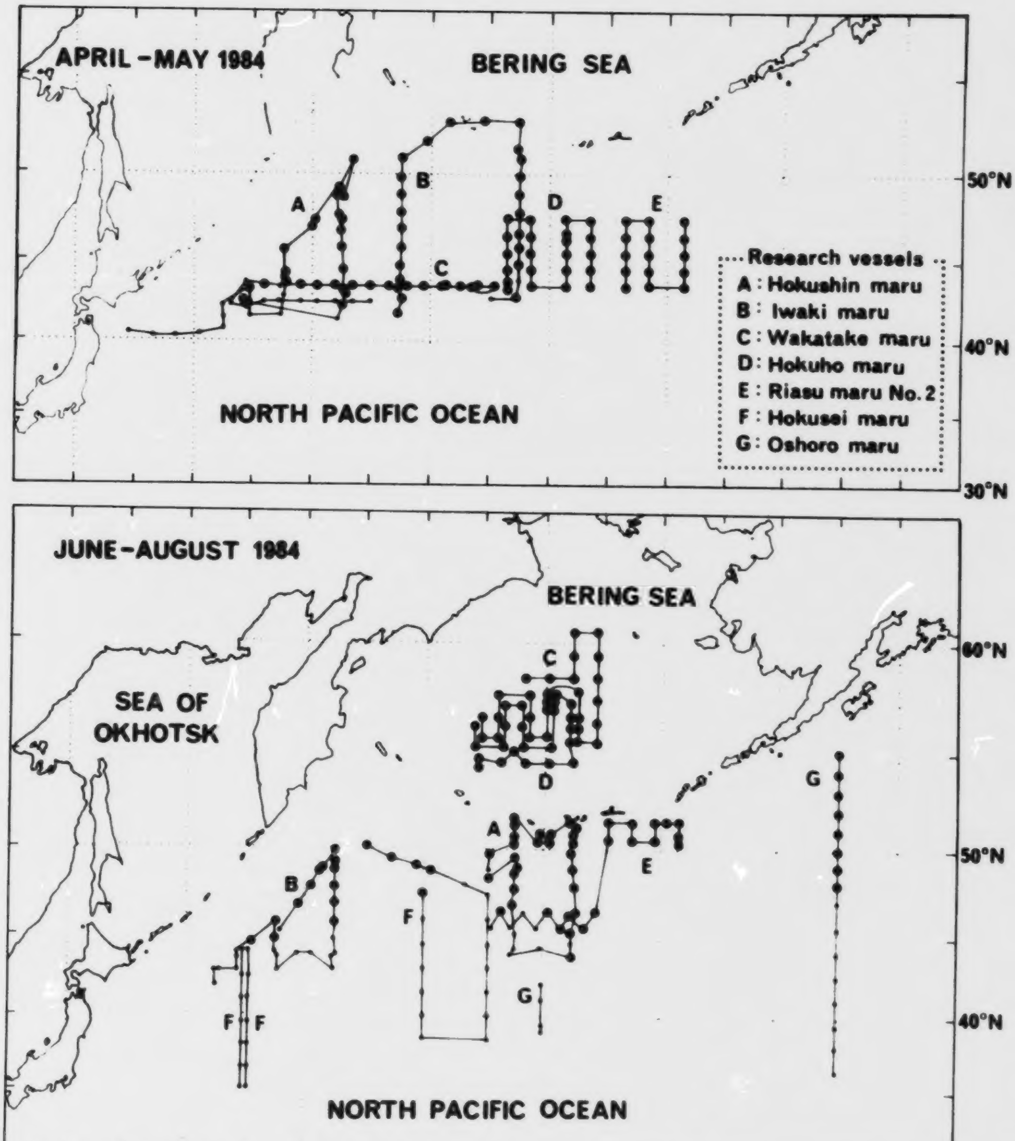
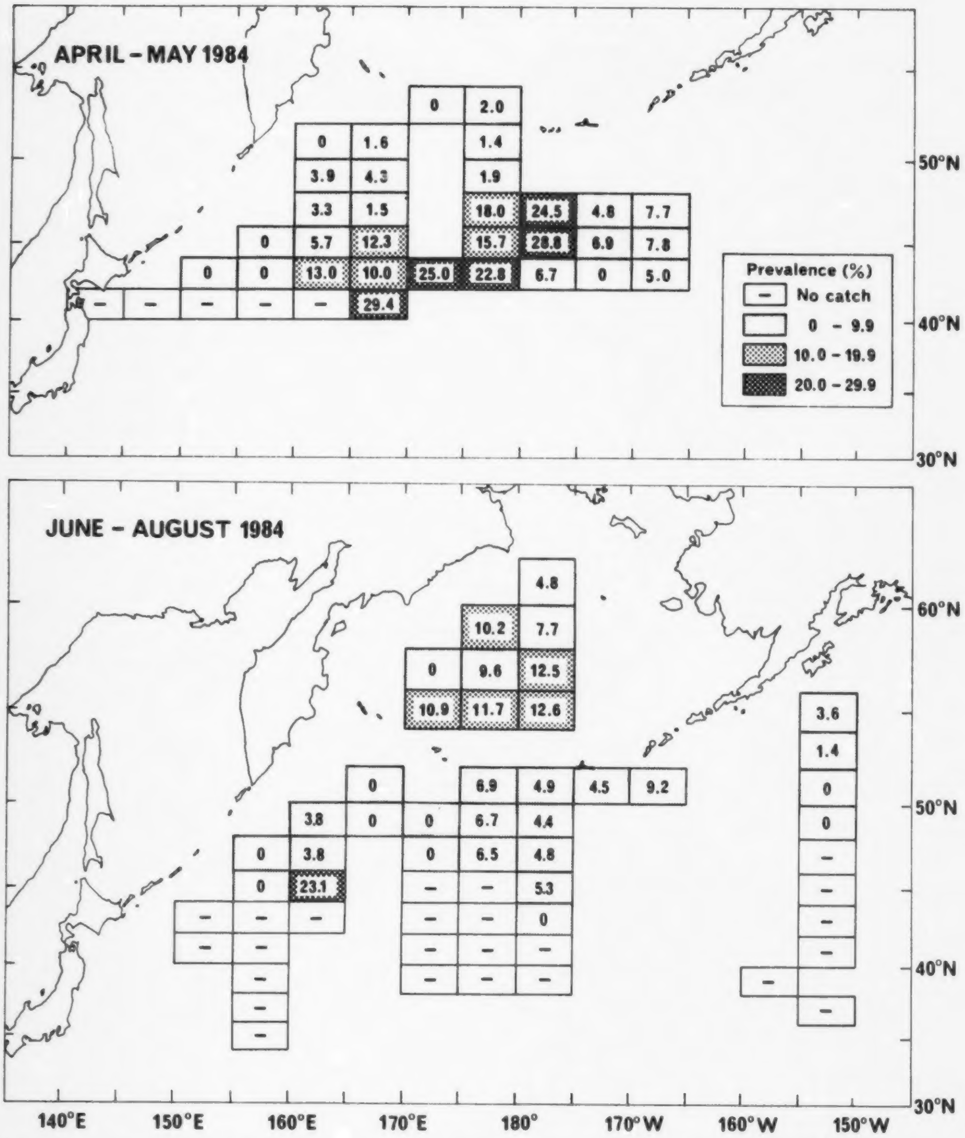

APRIL-MAY 1984
BERING SEA
A
B
C
D
E
NORTH PACIFIC OCEAN
Research vessels
A : Hokushin maru
B : Iwaki maru
C : Wakatake maru
D : Hokuho maru
E : Riasu maru No. 2
F : Hokusei maru
G : Oshoro maru
50°N
40°N
30°N
JUNE-AUGUST 1984
BERING SEA
SEA OF OKHOTSK
C
D
G
A
E
B
F
F
F
G
NORTH PACIFIC OCEAN
60°N
50°N
40°N
30°N
140°E
150°E
160°E
170°E
180°
170°W
160°W
150°W

FIG. 4. Cruise tracks and fishing locations of Japanese salmon research vessels in the North Pacific Ocean and Bering Sea in April–May (*top*) and June–August 1984 (*bottom*). Large and small closed circles indicate, respectively, fishing locations where sockeye salmon were, or were not, captured.

mostly immature and their average lengths ranged from 42 to 46 cm. Because, as mentioned above, prevalence was high in such immature medium-sized fish, their restricted distribution resulted in the high prevalences in these areas. A second noticeable feature was the decrease in prevalence from the south to the north in the areas between 160°E and 180°. In the southern latitudes with high prevalences, most fish were less than 50 cm in length and immature or maturing-I, whereas in the northern latitudes with low prevalences, fish were usually more than 50 cm in length and the proportion of maturing-II or -III fish increased markedly. Thus, the decrease in prevalence could be attributed to latitudinal changes in fish size and maturity. The lowest prevalences in the areas between 150° and 160°E, where no adhesions were observed, were also a reflection of the distribution of maturing large-sized fish.

In the summer months (June–August), surveys were more comprehensive than in the spring months and provided enough data to illustrate the ocean distribution of affected salmon in the North Pacific Ocean and Bering Sea. Most catches during this period were composed of immature medium-sized fish, although some returning, maturing large-sized fish were captured in the Gulf of Alaska and south and east of the Kamchatka Peninsula. The percentages of affected


APRIL - MAY 1984
0
2.0
0
1.6
1.4
3.9
4.3
1.9
3.3
1.5
18.0
24.5
4.8
7.7
0
5.7
12.3
15.7
28.8
6.9
7.8
0
0
13.0
10.0
25.0
22.8
6.7
0
5.0
–
–
–
–
–
29.4
Prevalence (%)
– No catch
0 - 9.9
10.0 - 19.9
20.0 - 29.9
50°N
40°N
30°N
JUNE - AUGUST 1984
4.8
10.2
7.7
0
9.6
12.5
10.9
11.7
12.6
3.6
1.4
0
6.9
4.9
4.5
9.2
0
3.8
0
0
6.7
4.4
0
0
3.8
0
6.5
4.8
0
23.1
–
–
5.3
–
–
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0
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–
60°N
50°N
40°N
30°N
140°E
150°E
160°E
170°E
180°
170°W
160°W
150°W

FIG. 5. Percentage prevalences of visceral adhesions in sockeye salmon caught in the North Pacific Ocean and Bering Sea in April–May (*top*) and June–August 1984 (*bottom*) by INPFC statistical areas.

salmon in samples from the North Pacific Ocean were mostly less than 10%, varying from 0 to 9.2% in 22 of 23 areas. The high prevalence (23.1%) in INPFC area E6044 was probably statistically insignificant because of the small sample size ($n = 13$). Prevalences in the Bering Sea were generally higher than those in the North Pacific Ocean, and five of nine INPFC areas in this region had prevalences of 10.2–12.6%.

Discussion

PREVALENCE

The dracunculoid nematode *Philonema oncorhynchi*, the cause of visceral adhesions in sockeye salmon, is a freshwater parasite, although it is commonly found in sockeye salmon caught on the high seas (Margolis 1963; Fig. 8). The intermediate host of this parasite is a freshwater copepod, *Cyclops bicuspidatus* (Platzer and Adams 1967; Ko and Adams 1969). Juvenile sockeye salmon become infected by feeding on infected copepods during their lake residence. The present study showed that the prevalence of visceral adhesions increased steadily with increasing freshwater age of fish. This is probably a reflection of higher intensities of infection of *P. oncorhynchi* in fish of longer freshwater residence. Konovalov (1971) examined the parasite fauna of sockeye salmon in Lake Dalnee, southern Kamchatka, and found an increase in prevalence and mean intensity of *P. oncorhynchi* with increasing host age. Margolis (1970) stated that the extent of the host reaction associated with the migration of the parasite must be related to the intensity of the infection. A similar suggestion was made by Nagasawa (1985).

Among fish of ocean ages 1–4, fish of age .2 were most frequently affected by visceral adhesions. Platzer and Adams (1967) noted that the migration of *P. oncorhynchi* from the tissues into the body cavity occurred in January when ex-

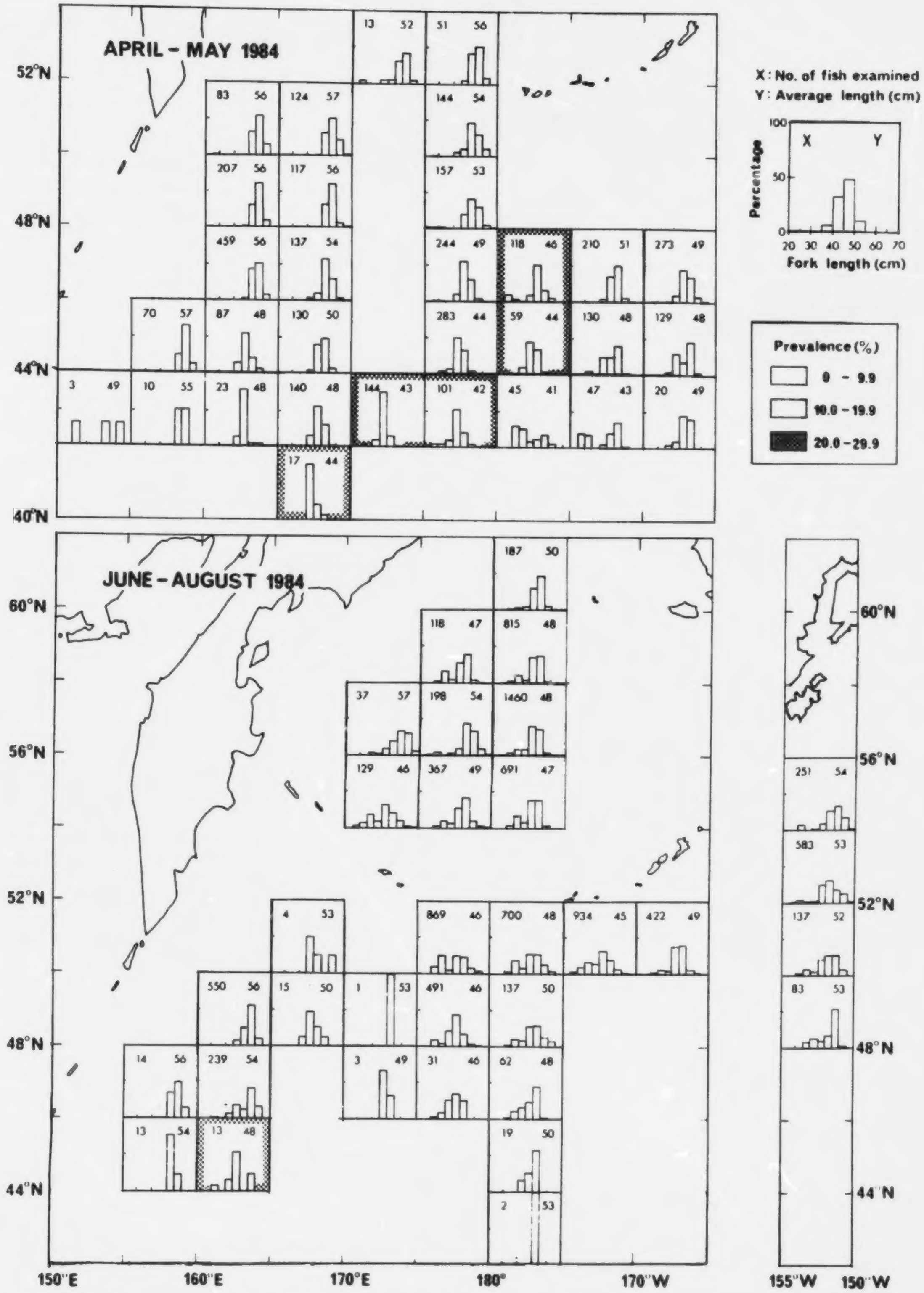

FIG. 6. Size frequency distribution of sockeye salmon caught in the North Pacific Ocean and Bering Sea in April–May (*top*) and June–August 1984 (*bottom*) by INPFC statistical areas.

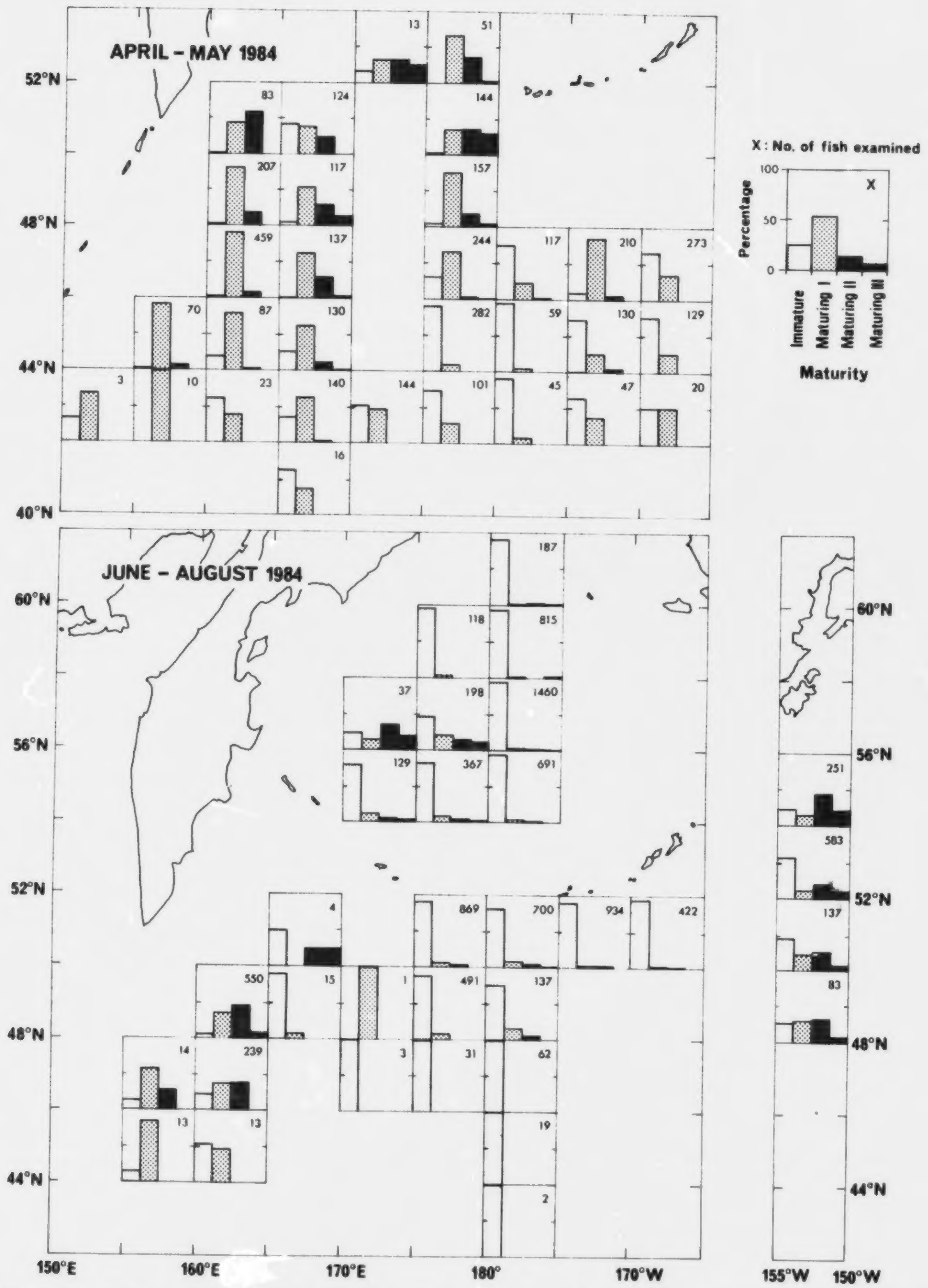

FIG. 7. Maturity frequency distribution of sockeye salmon caught in the North Pacific Ocean and Bering Sea in April–May (*top*) and June–August 1984 (*bottom*) by INPFC statistical areas.

perimental sockeye were 32 months old. This age corresponds to age 1.2 fish inhabiting the ocean. Since many sockeye salmon return to their natal rivers after spending two winters at sea, they would begin to secrete sex hormones actively in the second ocean winter. These hormones are believed to stimulate the migration and development of the parasite. The close relationship between the life cycle of *P. onchorhynchi* and host hormones was suggested by Platzer and Adams (1967), who advanced the hypothesis that larval production in *P. oncorhynchi* is synchronized with the host's maturation and production of sex hormones. This was recently confirmed by Bashirullah and Adams (1983). In addition, French (1965) recorded the highest prevalence (25%) of visceral adhesions in sockeye salmon caught in January and February 1964 from the North Pacific Ocean (49°–50°N, 174°W), which suggests that visceral adhesions are induced mainly during the winter season.

Male sockeye salmon were more frequently affected with adhesions than were females. Similar results were obtained by French (1965). Nagasawa (1985) stated that this sex-related difference in occurrence of adhesions may be influenced by the sockeye's sex hormones and that the timing of migration of *P. oncorhynchi* may be different between sexes. L. Margolis (Canada Dep. of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, personal communication), also suggested that there may be a stronger response to migrating *P. oncorhynchi* in males or a more rapid breakdown of adhesions in females.

EFFECTS ON SOCKEYE SALMON

The prevalence of visceral adhesions was highest in immature medium-sized fish, and decreased steadily with fish maturation and further growth. There could be two explanations for this decrease: one is the ocean mortality of affected salmon and the other is the disappearance of visceral adhesions. French (1965) noted that no external difference was evident between salmon with adhesions and normal salmon, and that food items in the former were similar to those in the latter. My preliminary observations on the stomach contents of sockeye with and without adhesions also showed no significant difference between them. No external signs such as emaciation and dark coloration of affected fish were observed during this study. Although *Philonema agubernaculum*, a species closely related to *P. oncorhynchi*, induces severe visceral adhesions in non-anadromous salmonids (Richardson 1936; Meyer 1954, 1958, 1960), there is no evidence that the adhesions caused mortalities of affected fish. L. Margolis (Canada Dep. of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, personal communication) stated that "if adhesions caused by *Philonema* seriously affect survival, then one would expect devastating effects on sockeye at the population level. The fact that sockeye escapements number in the tens of millions argues against such a large-scale effect". These observations indicate that visceral adhesions have no effect on the feeding activity, growth, and survival of high-seas sockeye salmon, and that the adhesions cause no ocean mortalities.

French (1965) found only one instance of salmon with adhesions among 14 223 sockeye from the inshore areas of North America during 1957–62 and noted that no adhesions were observed in many thousands of mature sockeye salmon in Alaskan canneries or from the spawning grounds. Platzer and Adams (1967) and Margolis (1970) stated that, since visceral adhesions were not found in their samples of mature salmon, the adhesions are transitory. Thus, if the adhesions cause no mortalities in sockeye salmon as suggested above, the absence of adhesions in mature sockeye is the consequence of their disappearance with fish maturation. This situation contrasts with the pathological conditions induced by *P. agubernaculum*. The visceral adhesions caused by this parasite persist in spawning salmonids. Richardson (1936) found a case of egg binding in infected brook trout (*Salvelinus fontinalis*). Meyer (1954, 1958, 1960) observed *P. agubernaculum*-induced adhesions in landlocked Atlantic salmon (*Salmo salar*) and brook trout and stated that the adhesions "may be so severe, especially in older fish, that neither normal spawning or stripping is possible".

The prevalence of adhesions in immature fish decreased markedly from spring to summer. A similar decrease occurred in fish 35–49 cm in length during the same period. This suggests that visceral adhesions disappear with season even in immature fish.

Bell and Margolis (1976) stated that "one of the factors affecting survival of progeny was the intensity of infection of the female parent with *Philonema oncorhynchi*". According to Margolis (1963; see Fig. 8), this parasite occurred in 76 of 77 sockeye samples from the high seas and the coast of North America with prevalences of 4–100% and mean intensities of 1–61. Konovalov (1971) also reported that 100% of mature sockeye salmon that had returned to Lakes Dalnee and Blizhnee in southern Kamchatka were infected with mean intensities of 62–83 *P. oncorhynchi* (1–305 worms/fish). Such high intensities of infection may suppress the enhancement of population levels of sockeye salmon stocks in North America and Asia.

OCEAN DISTRIBUTION

The results of this investigation showed that sockeye salmon with visceral adhesions were widely distributed in the North Pacific Ocean and Bering Sea. This wide distribution is not surprising because *P. oncorhynchi* has a similarly wide distribution throughout the North Pacific region (Fig. 8).

The oceanic distributional pattern of sockeye with adhesions changed from spring to summer. In spring, the major concentration of affected fish was in the areas between 165°E and 175°W from 40° to 48°N. This was due to the segregation of sockeye salmon according to maturity and size (age). During this period, the immature medium-sized fish were generally located south of the maturing large-sized fish in the central North Pacific Ocean. In summer, most of the maturing fish vacated the high seas because of their spawning migration and the immature fish became widely distributed in the North Pacific Ocean and Bering Sea. The relatively high prevalences of adhesions in sockeye in the Bering Sea probably resulted from the northward migration of immature fish with visceral adhesions. French et al. (1976) showed a similar northward movement of immature sockeye during summer. The generally lower prevalences in this season than in the spring were possibly due to the disappearance with time of visceral adhesions in immature fish.

The three major groups of sockeye salmon stocks originate in Asia (chiefly Kamchatka), western Alaska (Bristol Bay), and the northeastern Pacific coast of North America (Fig. 8). Sockeye caught west of 165°E are apparently of Asian origin. The discovery of visceral adhesions in those salmon, despite generally low prevalence, constitutes the first record of this disease for Asian stocks. Although western Alaska sockeye overlap in distribution with Asian sockeye in the North Pacific Ocean and Bering Sea (Margolis et al. 1966; French

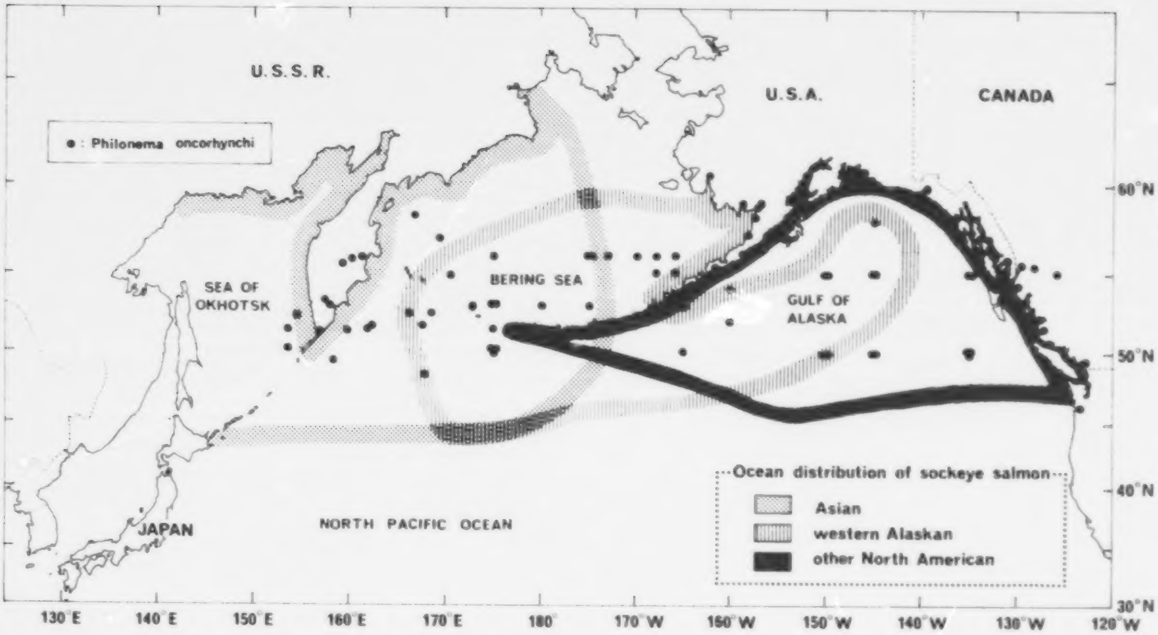

FIG. 8. Generalized ocean distribution of sockeye salmon from Asian, western Alaskan, and other North American areas (French et al. 1976) and capture locations of sockeye salmon infected with *Philonema oncorhynchi* (Margolis 1963; Konovalov 1971).

et al. 1976), most of the immature fish caught immediately south of the central Aleutian Islands during the summer months are considered to be of western Alaskan origin (Osako and Kato 1978). In the present study, the prevalences of visceral adhesions in sockeye from this area were found to be less than 10%. French (1965) obtained sockeye samples just south of Adak Island in the same region during August and September 1963 and found the disease in 9% of the samples. Since both immature Asian sockeye and immature western Alaskan sockeye intermingle in the Bering Sea during the summer months (Margolis et al. 1966; French et al. 1976), sockeye with adhesions caught in this sea probably originated from both regions. On the other hand, whether visceral adhesions occur in high-seas sockeye that originated from North American rivers tributary to the northeast Pacific is not clear, because western Alaskan sockeye and this stock group overlap widely in the Gulf of Alaska and the central North Pacific Ocean (French et al. 1976). However, the occurrence of *P. oncorhynchi* in sockeye from the northeastern Pacific coast (Fig. 8) suggests that visceral adhesions probably occur in fish of this stock group, as well.

Acknowledgments

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Some Effects of Suspended Fraser River Sediments on Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

SERVIZI, J. A., AND D. W. MARTENS. 1987. Some effects of suspended Fraser River sediments on sockeye salmon (*Oncorhynchus nerka*). p. 254–264. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The lethality of natural Fraser River sediments to underyearling sockeye salmon (*Oncorhynchus nerka*) increased with particle size. Fine sediments typical of those in suspension in the river were found to lodge in the gills of underyearlings and cause gill trauma at 3 148 mg • L^{-1} or 0.2 of the 96 h LC50 value. Sockeye smolts suffered a slight impairment in hypoosmoregulatory capacity when exposed 96 h to 14 407 mg • L^{-1} of fine sediment. Plasma glucose levels of adult sockeye increased 150 and 39% as a result of exposures to 1 500 and 500 mg • L^{-1}, respectively, of fine sediment. Suspended solids levels equal to those causing a stress response among adults have been recorded in the Fraser River during spawning migrations.

Résumé

SERVIZI, J. A., AND D. W. MARTENS. 1987. Some effects of suspended Fraser River sediments on sockeye salmon (*Oncorhynchus nerka*). p. 254–264. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La létalité des sédiments naturels du fleuve Fraser pour le saumon nerka (*Oncorhynchus nerka*) de moins d'un an augmente en fonction de la taille des particules. Les sédiments à grain fin qui sont en suspension dans les eaux fluviatiles se déposent dans les ouïes et causent un traumatisme à une teneur de 3 148 mg • L^{-1} ou à 0,2 de la CL50 après 96 h. Les smolts ont subi un léger affaiblissement de la capacité hypoosmorégulatoire après une exposition de 96 h à une teneur de 14 407 mg • L^{-1} en sédiments à grain fin. Les niveaux de glucose plasmatique chez le saumon nerka adulte ont augmenté de 150 % et de 39 % après des expositions à 1 500 et 500 mg • L^{-1}, respectivement, de sédiments à grain fin. Des teneurs en solides en suspension égales à celles causant une réaction de stress chez des adultes ont été signalées dans le fleuve Fraser au cours de la montaison.

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[1] Formerly International Pacific Salmon Fisheries Commission.

Introduction

The Fraser River rises in the Rocky Mountains and flows through the interior of British Columbia and the Coast Mountains to the Strait of Georgia (Fig. 1). The Fraser River is highly turbid for most of the year owing to erosion of river banks in the upper reaches. Sediments in the lower Fraser River are composed largely of quartz, feldspar, chlorite, mica, and amphibole (Mackintosh and Gardner 1966). Montmorillonoid is an important component of the clay fractions and kaolin is present in the coarse clay fractions of some samples (Mackintosh and Gardner 1966). Turbidity and suspended solids (SS) monitoring at Hell's Gate in the Fraser Canyon about 205 km from the mouth of the river indicate that maximum values occur during spring freshet. Suspended solids levels decrease throughout the summer and autumn to a minimum in winter and early spring. Minor peaks of SS may occur owing to landslides or heavy rains (Servizi and Burkhalter 1970).

Spawning migrations of sockeye salmon (*Oncorhynchus nerka*) occur in the Fraser River from July through November and the earlier migrants generally encounter higher values of SS. Seaward migrations of sockeye smolts occur in March, April, and May, as suspended solids increase with freshet.

Records kept by the International Pacific Salmon Fisheries Commission indicate that from time to time there have been unexplained losses of adult Early Stuart sockeye during migration through 650 km of the Fraser River to the spawning grounds 1 000 km from the mouth. Some data suggest a relationship between the loss of Early Stuart sockeye and turbidity or SS but the relationship is inconclusive. There are no indications that sockeye smolts have been adversely affected by SS during seaward migration in the Fraser, but the amount they can tolerate has not been documented.

The following study was conducted to provide information on the acute and subacute responses of underyearling, smolt, and adult sockeye salmon to suspended Fraser River sediments.

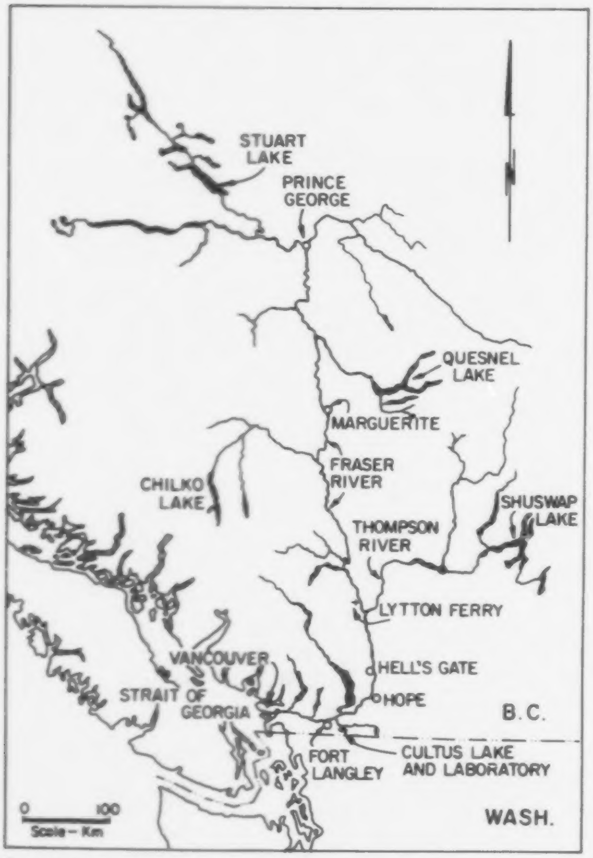

FIG. 1. Fraser River drainage.

Methods

SUSPENDED SOLIDS SAMPLES

Suspended solids and turbidity have been monitored regularly at Hell's Gate since 1965 by the International Pacific Salmon Fisheries Commission and analyzed according to Standard Methods (1960, 1965, 1971, 1975, 1980, 1985). In addition, an intensive suspended solids monitoring program was conducted during summer 1983, coincident with upstream migration of Early Stuart sockeye. Particle size analyses were conducted on peak SS samples from Hell's Gate, Lytton Ferry, and Marguerite. Particle size was measured with calipers from photomicrographs of each sample. The size of particles was obtained by calibrating calipers with a photomicrograph of the stage micrometer for each magnification. Each particle was measured along its longest and shortest axis and particle size expressed as the geometric mean diameter, GMD (square root of the product of the longest and shortest axes).

SEDIMENT SOURCES FOR BIOASSAYS

Sediments were collected from sandbars between Hope and Ft. Langley at low river flow. Sites containing fine, intermediate, and coarse sediments were chosen to provide a range of particle sizes for tests. Samples were air dried and a portion screened into four particle size ranges (<74, 75–149, 150–295 and 180–740 μm) with Tyler Standard screens for tests of underyearling sockeye. All other tests were made with fine sediment as collected near Ft. Langley. Particle size analyses were performed on the <74 and 180–740 μm screened samples and the sample of fine sediment from Ft. Langley.

UNDERYEARLING BIOASSAYS

Bioassays of underyearling sockeye were conducted in 1983 in inverted cone shaped vessels 42 cm in diameter by 52 cm high and fitted with a screen to keep fish in the upper 26 cm. Pumps recirculated water and sediment from the cone apex to the water surface with part of the pump flow directed to create peripheral velocity of approximately 15 cm • s^{-1} for test fish orientation. The water volume was 30 L. Four particle size ranges of sediment were bioassayed. Each particle size range was bioassayed once and consisted of five sediment concentrations and a sediment-free control with 10 fish in each vessel.

Sockeye underyearlings reared at Cultus Lake laboratory were used in bioassays. All fish were fed Oregon Moist Pellet diet but were not fed for one day prior to bioassays. Average weight of test fish ranged from 0.78 to 1.5 g during the bioassay period. The loading weights of fish in test vessels ranged from 0.26 to 0.50 g • L^{-1}.

During bioassays, samples were withdrawn daily from the surface and about 14 cm depth of each bioassay vessel for measurement of SS (Standard Methods 1980). Temperature was measured daily and dissolved oxygen (DO) was measured once in each vessel during each bioassay. DO was measured with a YSI Model 54 DO meter which had been calibrated by the alkali-azide-iodide titrametric procedure of the Winkler method (Standard Methods 1980). Since test fish could not be seen in the opaque test mixtures, daily mortality checks were done by hand probing. Acute toxicities of suspended sediments were expressed as 96 h LC50's (Standard Methods 1980). Following each 96 h test, all surviving fish were transferred to histological fixative (Bouins solution) and then to 70% ethanol 24 h later. These fish were later processed for histological examination of gills.

To test for possible acute toxicity from contaminants leached from Fraser River sediment, fish were exposed to supernatant from a mixture of sediment and water. The supernatant was made by recirculating a 40 000 mg • L^{-1} mixture of fine Fraser River sediment and water in one of the bioassay vessels for 24 h. This mixture was allowed to settle 16 h before the supernatant was decanted into another bioassay vessel for the 96 h fish exposure.

Smolt Bioassays and Seawater Challenge

About 500 Cultus Lake smolts were captured in the outlet stream in mid-April 1985 during downstream migration. These fish were held in a 135 L circular pond and fed Oregon Moist Pellet once daily. Fish were starved for 1 day prior to each bioassay.

Each of the bioassays consisted of a 96 h static exposure to sediment-water mixtures or sediment-free Cultus Lake water in eight of the same vessels used for underyearlings except that the water volume was 36.5 L. Four test vessels contained sediment-water mixtures at the same nominal concentration while the remaining four contained sediment-free Cultus Lake water. Each test vessel contained five smolts. Fine sediment ($<$74 µm) was used in the smolt bioassays because the particle size distribution closely approximated size distribution measured in Fraser River samples.

TABLE 1. Sockeye smolts; sediment concentrations to which smolts were exposed for 96 h and seawater challenge schedule.

Post capture day	Sediment exposure 96 h (mg • L^{-1})	Seawater challenge 48 h salinity %	Temp °C
11	7 477	30.0	6.2
11	0 (control)	30.0	6.2
18	2 678	26.5	6.5
18	0 (control)	26.5	6.5
25	14 407	27.0	6.5
25	0 (control)	27.0	6.5
32	1 261	27.5	7.0
32	0 (control)	27.5	7.0

During bioassays using smolts, mortality checks, DO, temperature, and SS measurements were made on the same schedule and by the same methods as those described for underyearlings. Ammonia nitrogen was measured periodically by the method of Harwood and Kuhn (1970). Following 96 h exposure to sediments, each group of fish, including controls, was transferred immediately to a 50 L aquarium for a further 48 h in either sediment-free sea water or fresh water (Table 1).

Sea water was transported weekly in a fiberglass lined tank from the Department of Fisheries and Oceans, West Vancouver Laboratory to Cultus Lake laboratory. The density of each load of sea water was measured using a hydrometer and salinity was obtained from a graph relating salinity and density.

After each 48 h seawater challenge test, smolts were anesthesized one group at a time in an aerated solution of 2, phenoxy-ethanol (0.5 mL • L^{-1}) prior to blood sampling. Blood was collected in heparinized micro-hematocrit tubes from the severed caudal peduncle and kept on ice prior to centrifuging for three minutes at 11 500 RPM in a 4°C centrifuge. Hematocrits were measured on a micro-hematocrit reader. Elapsed time from the beginning of blood sampling to centrifuging was less than 10 min for each group of fish. The red blood cell portion of the micro-hematocrit tubes was broken off and the plasma blown into micro-test tubes for frozen storage prior to plasma chloride determination. Plasma chloride was measured with a Buchler chloridometer using 10 µL aliquots for each determination. Smolts were also weighed and a piece of body muscle from the lateral area was removed for measurement of per cent moisture. Samples for body moisture determination were blotted dry and weighed before and after drying for 24 h at 103–105°C. Gill samples were excised for histological examination by the methods previously described for underyearlings.

Adult Tests

Adult sockeye studies consisted of two experiments; the first in July 1984 using males and females of the Early Stuart race and the second in November using Cultus Lake males. Fine sediment ($<$74 µm) was used in tests of adults because the particle size distribution closely approximated the size distribution measured in a Fraser River water sample from Hell's Gate.

Early Stuart fish were exposed nine days to about 1 500 mg • L^{-1} of SS which was within the high range expected during migration of this race through the Fraser River. Water temperature was increased in each tank over the exposure period to simulate river temperatures normally encountered by this race during migration in the Fraser. Cultus sockeye were exposed for 15 days at about 8°C to sediment concentrations (462 and 553 mg • L^{-1}) similar to the maximum mean concentration during early summer migration of sockeye in the Fraser River.

Early Stuart sockeye were captured at Hell's Gate fishways and transported to the Cultus Lake laboratory. Cultus sockeye were captured at a counting weir near the outlet of Cultus Lake.

Fish were exposed in annuluses measuring 30 cm wide by 80 cm deep with an inside diameter of 1.2 m. Both control and experimental tanks were in duplicate with 10 fish in each tank. Sediment was continuously added to the experimental tanks by augers which directed dried sediment into a container where it was mixed with water before entering the tanks. Water inflow rate during the Early Stuart sockeye experiment was 12 L • min^{-1}. Oxygen was added to maintain DO. Inflow during the Cultus sockeye experiment was 24 L • min^{-1} and oxygen addition was not required to maintain DO. Water (controls) or water–sediment mixtures were recirculated in each tank by a 1 HP pump. Recirculation reduced settling of sediments and provided a velocity of approximately 30 cm • s^{-1} for the test fish to swim against.

During tests, water inflow rate, DO, temperature and mortality were checked daily. Water samples were taken twice daily for SS determination; ammonia nitrogen was measured periodically by the method of Harwood and Kuhn (1970). Un-ionized ammonia was calculated according to Trussel (1972). Total gas pressure (TGP) was measured with a Novatech Model 300B tensionometer once in each tank during each experiment.

At the termination of each experiment, fish were stunned by a blow to the head. Blood samples were taken from each fish for measurement of hematocrit, leucocrit, and plasma glucose. Samples for hematocrit and leucocrit were processed in the same manner as that described for smolts except that a magnifying glass was used in reading leucocrit values. Blood samples for plasma glucose determination were withdrawn from the caudal vein via a 7 mL heparinized vacutainer. These samples were centrifuged and the plasma decanted to test tubes for frozen storage. Plasma glucose was measured later by the ortho-toluidine method of Hyvarinen and Nikkila (1962). Tanks were sampled individually to minimize the effect of fright response on plasma glucose levels. Ten minutes or less were required to sample fish in each tank. A gill sample was excised from each fish and preserved for later histological examination as described earlier for juvenile sockeye.

Student's "*t*" test was used for all statistical comparisons.

Results

PARTICLE SIZE ANALYSES

Fine sediments (<74 µm) from Ft. Langley used in bioassays of underyearlings, adults, and smolts were similar in particle size distribution to that of suspended sediment in samples from Hell's Gate (Fig. 2). Samples from Lytton Ferry and Marguerite contained a slightly greater amount of particles larger than 5 µm. Particles in the coarse screened sediment ranged from 180 to 740 µm with a median size in the 420 to 440 µm range, which was at least 86 times larger than the fine sediment (Fig. 3).

Besides size, angularity and hardness of sediment particles are suspected to play a role in causing trauma in fish gills. Hardness of sediment particles was not investigated in this study. Angularity was judged subjectively from photomicrographs of each sediment. In general, angularity of particles appeared similar in each of the test sediments (Fig. 4). A high proportion of particles in each sample would be described as angular to subangular (Muller 1967).

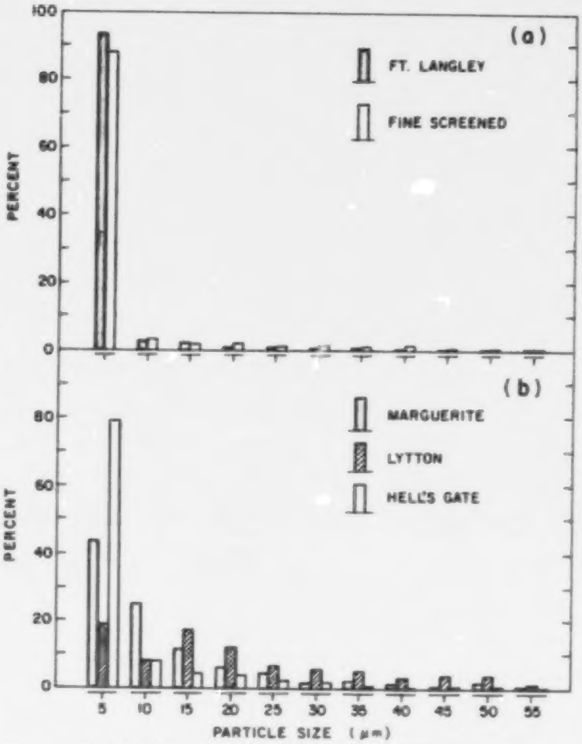

FIG. 2. Particle size distribution (Geometric Mean Diameter) for (a) test sediments derived from Ft. Langley and Tyler standard screening of Fraser River sediments and (b) samples of Suspended Solids from the Fraser River at Marguerite, Lytton, and Hell's Gate.

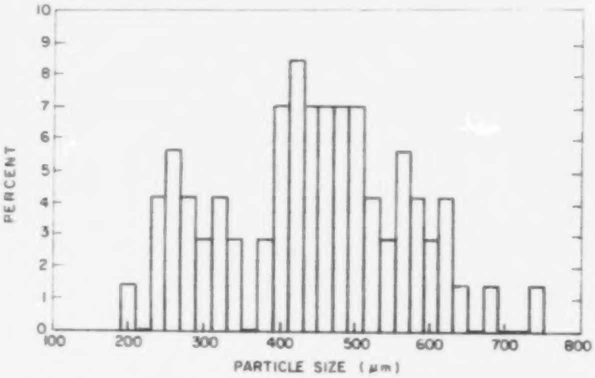

FIG. 3. Coarse sediment particle size distribution (Geometric Mean Diameter).

UNDERYEARLING BIOASSAYS

During bioassays, temperature ranged from 7.8 to 8.3°C, DO from 10.3 to 11.1 mg • L^{-1}, DO saturation from 88 to 93%, and pH from 7.8 to 8.2. Fish were unaffected by exposure to the supernatant from 40 000 mg • L^{-1} fine sediment.

The 96 h LC50's decreased with increasing particle size (Fig. 5). For the fine sediment, which was similar in particle size to SS in the Fraser River, the 96 h LC50 was 17 560 mg • L^{-1}. Behavior of test fish could not be quan-

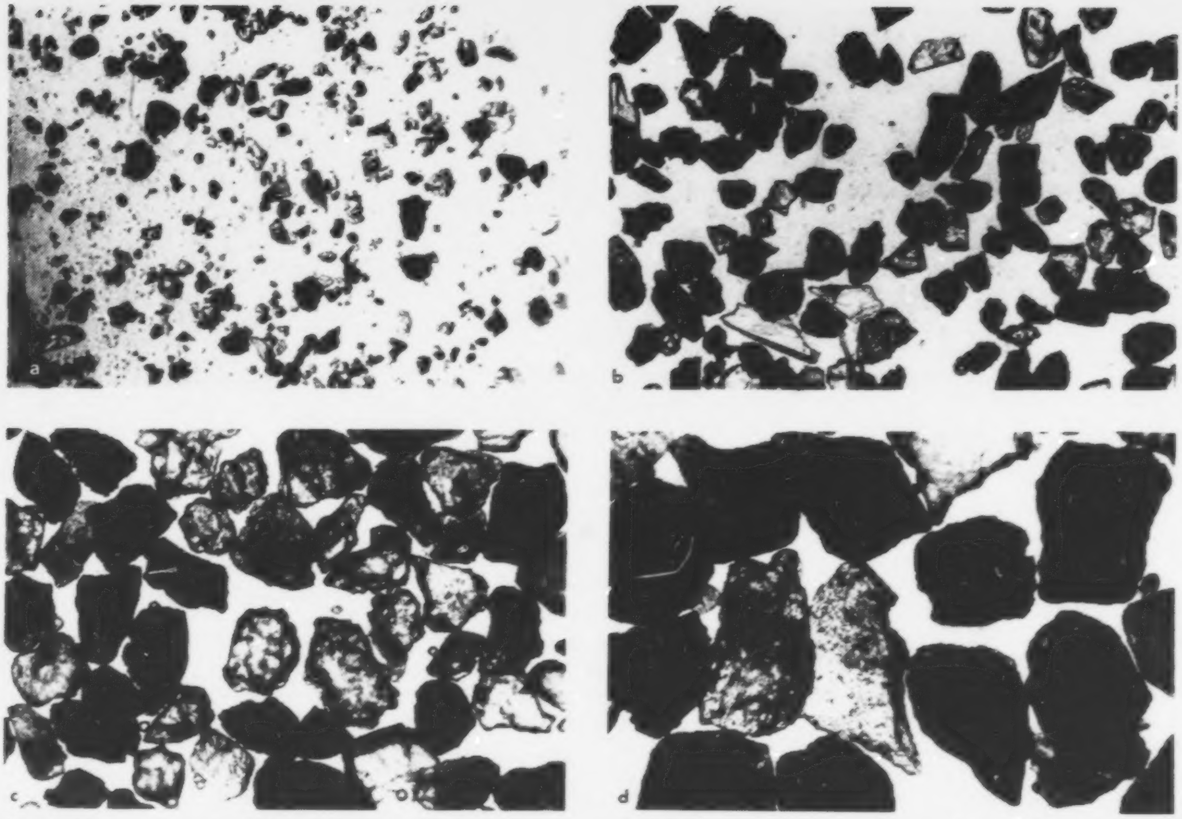

FIG. 4. Photomicrograph at 80 × of test sediments used in bioassays of underyearlings (a, b, c, and d), smolts and adults (a): (a) Fine (<74 µm), (b) medium-fine (75–149 µm), (c) medium-coarse (150–295 µm), and (d) coarse (180–740 µm).

titatively measured owing to the opacity of the test mixtures. However, fish were frequently observed on the water surface in the higher concentrations in each bioassay, but respiratory distress such as gulping was not observed.

Histological examination of gill tissue excised from surviving fish revealed some fine sediment particles between the gill lamellae. Medium-fine, medium-coarse, or coarse particles were not observed between the gill lamellae. No excess mucus was observed on underyearling gills in either gross or histological examinations. Trauma was observed at both lethal and non-lethal concentrations of sediments (Table 2). Gill injuries were noted at sediment concentrations equal to 18 and 55% of the 96 h LC50 values for fine and medium-coarse sediments, respectively, but no gill trauma was observed at 85% of the 96 h LC50 for medium-fine sediment. In general, hypertrophy and necrosis were seen in survivors from both lethal and nonlethal concentrations of sediment, except that hyperplasia and epithelial separation were also observed in survivors from a concentration of medium-fine sediment equal to 1.21 times the 96 h LC50. Observations of gill trauma caused by fine sediment at sublethal levels are of particular interest since the particle size distribution of this sediment was similar to that found in Fraser River water samples.

Pathological conditions or obvious parasitic infections of gills were not observed in control or test fish.

SOCKEYE SMOLT BIOASSAYS

Temperature and DO ranged from 6.2 to 7.0°C and 10.8 to 11.0 mg • L^{-1}, respectively, during smolt bioassays while pH ranged from 7.8 to 8.2. The greatest ammonia nitrogen concentration measured was 162 µg • L^{-1}, after 72 h exposure in 14 407 mg • L^{-1} sediment. At the ambient temperature and pH, this concentration of ammonia nitrogen yields 1.44 µg • L^{-1} of un-ionized ammonia; well below the harmful level (Haywood 1983).

Mean smolt weight of 5.24 g translated into a mean bioassay loading of 0.7 g • L^{-1}. Although this loading is greater than that recommended by Sprague (1969), it is less than the 0.8 g • L^{-1} maximum recommended by Standard Methods (1980,1985). Recommendations for maximum bioassay loading are based in large part on considerations of adequate DO, ammonia nitrogen buildup from the test fish, and toxicant loss via uptake by test fish. The mean bioassay loading in these tests was acceptable, because the sediment tested was of an inert inorganic nature not subject to loss during bioassays, and measured DO was high and un-ionized ammonia low.

No mortalities occurred during four day bioassays among control or experimental groups. The highest sediment concentration tested was 14 407 mg • L^{-1}. Furthermore, no mortalities occurred when test or control fish were transfer-

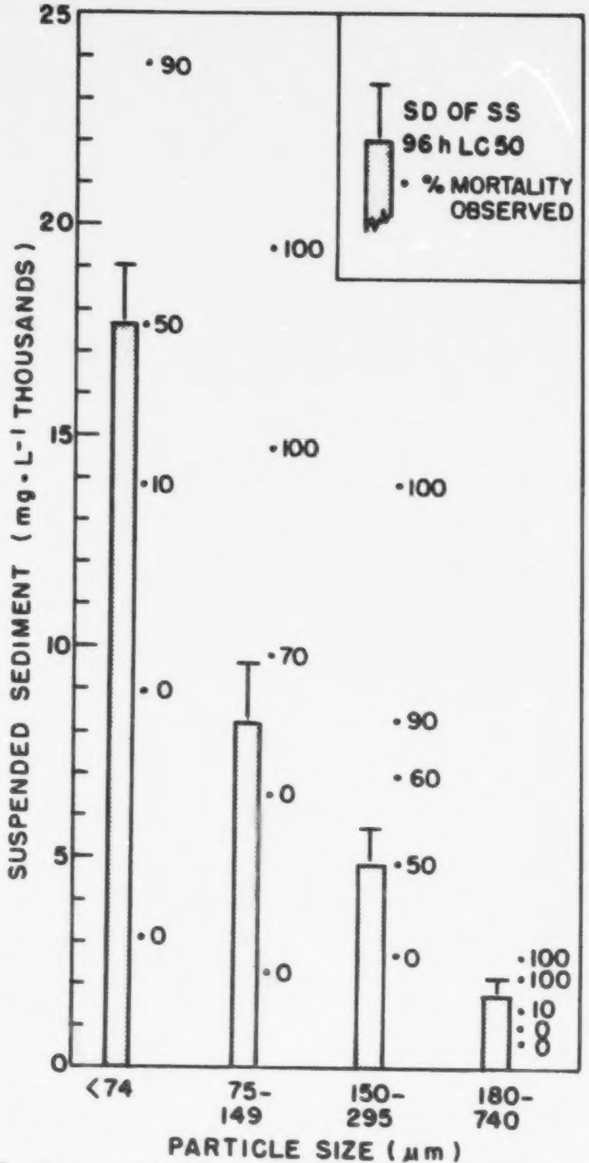

FIG. 5. Acute toxicity to underyearling sockeye of four particle size ranges of suspended sediments.

red to sea water or sediment-free fresh water for 48 h.

Smolts were frequently observed with their backs partly out of the water at 14 407, 7 447, and 2 678 mg • L^{-1} sediment but not at 1 261 mg • L^{-1}. Respiratory distress was not observed. More detailed observations of smolt behavior were not possible owing to the opacity of test mixtures.

Smolts which had been exposed to sediments were consistently pale in color when transferred to sea water or sediment-free fresh water following the 96 h bioassays. However, within less than 1 h these fish all darkened in color and were indistinguishable from controls.

Body moisture of control groups in sea water were equal even though seawater entry occurred at 11 to 32 days after capture (Table 3). Exposure to 7 447 and 2 678 mg • L^{-1} sediment did not cause a change in body moisture when smolts were transferred to sea water. However, smolts exposed to 14 407 and 1 261 mg • L^{-1} sediment had a significantly lower body moisture when transferred to sea water than their respective control groups ($P<0.01$ and <0.05 for 14 407 and 1 261 mg • L^{-1}, respectively). For body moisture to be lower in smolts transferred to sea water after exposure to 1 261 mg • L^{-1} sediment appears contrary to results at 7 447 and 2 678 mg • L^{-1} sediment. However, since 11 to 32 days elapsed between capture and transfer to sea water, those smolts transferred last (after exposure to 1 261 mg • L^{-1} SS) may have had a reduced hypoosmoregulatory capacity and thus were more easily stressed by sediment..

Hematocrit was in the range 40.9 to 45.5% but there were no sediment related significant differences between any of the experimental and control groups after transfer to sediment-free sea water or fresh water.

For control groups transferred to sea water up to 18 days after capture, mean plasma chlorides were about 132 mEq • L^{-1} (Table 4). However, for controls transferred to sea water at 25 days or more, mean plasma chlorides were elevated to about 143 mEq • L^{-1}. In addition, the standard deviation was increased for transfers to sea water after 25 days. This elevation in plasma chloride and increase in standard deviation suggests that hypoosmoregulatory capacity decreased slightly for control groups over the course of the testing program. It is noteworthy, however, that plasma chlorides remained below 170 mEq • L^{-1}, the concentration above which hypoosmoregulatory stress may occur (Clarke and Blackburn 1977).

When smolts exposed to 7 447 mg • L^{-1} sediment were transferred to sea water 11 days after capture, plasma chlorides were elevated significantly above the corresponding control group (Table 4). There were no significant differences in plasma chloride between experimental and control groups for the remaining tests. However, standard deviations for the experimental groups were greater than for control groups at each sediment concentration. These data suggest that osmoregulatory performance was reduced slightly owing to exposure to suspended sediments. However, in no case did capacity decrease to a level where plasma chlorides reached the acute stress level of 170 mEq • L^{-1}.

Histological examination of gills of control and experimental smolts did not reveal any trauma, excess mucus or trapped sediment particles. Smolts had been in sediment-free sea water or fresh water for 48 h when sampled and would have had an opportunity to clean particles from the gills.

ADULT SOCKEYE

Early Stuart — Dissolved oxygen fluctuated in each of the tanks during the nine day test. Concentrations ranged from 8.4 to 16.4 mg • L^{-1} as a result of malfunctioning oxygen regulators. Oxygen concentrations ranged from 73 to 140% of saturation. High oxygen saturation values raised concern that total gas pressure (TGP) may exceed safe levels, but measurements made in each tank at times when oxygen concentrations were at or near maxima indicated TGP did not exceed 100%. Temperatures were increased in each tank from 8.5°C on the first day to 13.5-14.5°C on the last day

TABLE 2. Underyearling sockeye bioassays: Summary of histopathological effects of sediments on gills of bioassay survivors.

Particle size (μm) Suspended sediment (mg • L^{-1})[a]	Fraction of 96 h LC50	Hyper-plasia	Hyper-trophy	Separ-ation	Necro-sis
Fine (<74)					
3 143 SL	0.18	0	+	0	+
17 560 L	1.00	0	+	0	0
23 790 L	1.35	0	+	0	+
Med. Fine (75–149)					
6 949 SL	0.85	0	0	0	0
9 850 L	1.21	+	+	+	+
Med. Coarse (150–295)					
2 688 SL	0.55	0	+	0	+
6 991 L	1.43	0	+	0	+
Coarse (180–740)					
1 465 SL	0.88	0	+	0	+
3 359 L	2.01	0	+	0	+

[a] SL = sublethal concentration; L = lethal concentration.

of testing. Diurnal temperature fluctuations of 0.5 to 1.0°C occurred owing to very hot weather.

Ammonia nitrogen measurements made on three separate occasions in each tank indicated concentrations ranged from 80 to 174 μg • L^{-1}. These concentrations yield un-ionized ammonia concentrations in the range 0.36 to 1.10 μg • L^{-1} at ambient temperatures and pH's. These concentrations of Based on the foregoing, some mortality associated with disease was anticipated in the 9-day exposure period. However, mortalities did not occur among control or experimental groups. Gross examination of the gills of fresh dead fish at conclusion of the test did not reveal any infections or other abnormalities. Histopathological examination of gills did not reveal any marked pathological condition or excess mucus in either control or sediment-exposed fish, but sediment particles were observed between gill lamellae of the latter. Adult fish were observed twice daily but respiratory distress was not seen. Subsurface observations in water–sediment mixtures were not possible.

For Early Stuart sockeye, leucocrit averaged 1.2% in each of the control and sediment exposed groups (Table 5). However, sediment-exposed fish had hematocrits which were significantly greater than control fish ($P<0.001$). Mean ammonia are considered safe for salmonids (Haywood 1983).

Sexually maturing Pacific salmon are often difficult to use as experimental animals owing to their degenerating physiological condition. Infections associated with this degenerating state often result in prespawning mortality in both the natural environment (Williams et al. 1977) and probably more so in the crowded experimental environment. plasma glucose of control groups 1 and 2 averaged 97.5 and 164.4 mg • mL^{-1} and were significantly different ($P<0.001$). The reason for elevated plasma glucose in control group 2 is quite likely related to sampling procedure. Spatial arrangement of the two control tanks was such that fish in the second control were severely disturbed while fish were being sampled from the first. Disturbances such as netting can cause secondary stress effects such as hyperglycemia in fish (Mazeaud et al. 1977). Thus, it is possible that the greater plasma glucose values in control 2 are a reflection of fright response. However, experimental groups 1 and 2 had mean plasma glucose concentrations significantly greater than control 1 ($P<0.01$).

Cultus Adult Males — Temperature was maintained at 7.5 to 8.9°C during the 15-day test. Since the inflow rate to each

TABLE 3. Body moistures of sockeye smolts transferred to sea water or fresh water after exposure to SS.

Post capture days	Suspended sediment (mg • L^{-1})	Mean body moisture % ± S.D.	
		Sea water	Fresh water
13 (11)	7 447	77.03[d] ± 1.93	77.16 ± 0.95
	0	77.49 ± 1.71	77.05 ± 1.34
20 (18)	2 678	76.26[d] ± 2.36	76.85 ± 0.61
	0	76.52 ± 0.88	76.61 ± 0.80
27 (25)	14 407	75.15[b] ± 1.40	77.60 ± 1.28
	0	77.92 ± 2.36	77.93 ± 1.08
34 (32)	1 261	76.55[c] ± 1.24	78.03 ± 2.09
	0	77.52 ± 0.77	78.17 ± 1.49

[a] First number is time from capture to sampling; number in parantheses refers to time from capture to transfer to sea water or fresh water.

[b] Significantly less than control group ($P<0.01$).

[c] Significantly less than control group ($P<0.05$).

[d] Not significantly different from control group.

TABLE 4. Plasma chlorides of sockeye smolts transferred to sea water or fresh water after exposure to SS.

Post capture days	Suspended sediment (mg • L^{-1})	Mean plasma chloride mEq • L^{-1} ± S.D.	
		Seawater	Freshwater
11	7 447	139.5[a] ± 9.9	133.8 ± 2.6
	0	131.2 ± 4.8	131.3 ± 5.4
18	2 678	135.6[b] ± 7.1	131.0 ± 2.6
	0	132.0 ± 1.8	129.5 ± 3.5
25	14 407	153.6[b] ± 12.8	132.4 ± 3.8
	0	142.8 ± 8.2	129.4 ± 6.0
32	1 261	140.8[b] ± 16.3	130.6 ± 2.6
	0	142.7 ± 10.5	126.3 ± 1.9

[a] Significantly greater than control group ($P<0.05$).
[b] Not significantly different from control group.

tank was 24 L • min^{-1}. DO was maintained without oxygenation or aeration. Measured DO ranged from 8.3 to 10.4 mg • L^{-1} and oxygen saturation from 70 to 87%. Ammonia was not measured since results of tests with Early Stuart adults indicated that total ammonia nitrogen and un-ionized ammonia concentrations were well below harmful levels at 12 L • min^{-1} inflow.

Suspended solids averaged 462 and 553 mg • L^{-1} for experimental groups 3 and 4, respectively (Table 5). Although a greater average SS was measured in experimental group 4, statistical comparison indicated no difference existed. Lack of visibility in the sediment-water mixtures precluded any subsurface observations of behavior. There was no surfacing behavior to suggest respiratory distress.

Mortalities occurred in each tank except control 4. Each of the four mortalities in control 3 had fungused gills and yellow coloured lesions similar in appearance to lesions caused by *Flexibacter columnaris* infection. Only one of four mortalities in the experimental groups was observed before tanks were drained after live fish were sampled at the conclusion of the test. This fish also had fungused gills and lesions similar to those observed in control mortalities. The remaining three were too decayed to examine.

For Cultus male sockeye, there were no significant differences among mean leucocrit values for experimental and control groups (Table 5). The mean hematocrit for controls, 34.0%, was not significantly different from that of either of the experimental groups. Mean plasma glucose of experimental groups was significantly greater than that of controls ($P<0.001$). Gross examination of gills of survivors at termination of the test did not reveal any of the lesions observed on gills of mortalities in both control and experimental groups. Histopathological examination of gills from both control and experimental Cultus Lake fish did not reveal any pathological conditions or excess mucus attributable to sediment exposures. Sediment particles were observed between the gill lamellae of all adults exposed to sediments, but fewer particles were observed among Cultus Lake than among Early Stuart sockeye.

TABLE 5. Adult sockeye bioassays: mortality, leucocrit, hematocrit, and plasma glucose concentration of adult sockeye in control and SS tanks.

Suspended sediment (mg • L^{-1})	Group	Mort. (%)	Leucocrit (%)	Hematocrit (%)	Plasma glucose (mg • L^{-1})
			Early Stuart		
<5	Control 1	0	1.2 ± 0.4[a]	36.6 ± 1.2	97.5 ± 13.9
<5	Control 2	0	1.2 ± 0.2	39.1 ± 4.3	164.4 ± 42.6[g]
1 528 ± 218	Expt'l 1	0	1.2 ± 0.3	41.3 ± 5.0[b]	226.2 ± 113.7[c]
1 626 ± 516	Expt'l 2	0	1.2 ± 0.2	41.7 ± 3.8[b]	257.8 ± 110.1[c]
			Cultus Lake		
<5	Control 3	40	0.5 ± 0.5	32.7 ± 6.5	107.9 ± 19.1
<5	Control 4	0	0.7 ± 0.2	35.3 ± 4.1	106.4 ± 11.1
462 ± 126	Expt'l 3	30	0.9 ± 0.4	29.4 ± 5.2[d]	143.4 ± 14.0[f]
553 ± 187	Expt'l 4	10	0.8 ± 0.3	38.2 ± 7.3[d,e]	154.0 ± 44.8[f]

[a] Means ± one standard deviation.
[b] Significantly greater than controls ($P<0.001$).
[c] Significantly greater than control 1 ($P<0.01$).
[d] Not significantly different from controls ($P<0.05$).
[e] Significantly greater than experimental 3 ($P<0.05$).
[f] Significantly greater than controls ($P<0.001$).
[g] Significantly greater than control 1 ($P<0.01$).

Discussion

Coarse and medium-coarse sediment particles were not observed on gill lamellae of underyearling sockeye at lethal or sublethal SS concentrations. However, fine sediment particles were observed on gill lamellae of underyearlings at both lethal and sublethal concentrations. In the case of underyearlings, gill trauma was observed at lethal concentrations in the four particle-size ranges tested. Fine sediment particles were also observed between the lamellae of adult gills at 1 500 and 500 mg • L^{-1}, more so at the former concentration, but were not accompanied by mortality or gill trauma. Thus, mortality and gill trauma in underyearlings and adults were not necessarily associated with presence of sediment particles lodged in the gills. Smolts did not have sediment particles lodged on the gills or exhibit gill trauma even when exposed to fine sediment concentrations four times those causing gill trauma and particles lodging in the gill lamellae of underyearlings. However, following sediment exposures, smolts were held 48 h in sediment-free water prior to sampling and during this time sediment particles may have been dislodged and smolts may have had time to recover from gill trauma.

Elevated hematocrit may indicate a response to hypoxic conditions or anoxia in salmonids (Holeton and Randall 1967; Swift and Lloyd 1974). Elevated hematocrits were observed in Early Stuart adults exposed nine days to 1 500 mg • L^{-1} fine sediment but not in Cultus adults exposed 15 days to 500 mg • L^{-1}. Sediment-induced hematocrit increase was also shown for white perch (*Roccus americans*), hog chokers (*Trinectes maculatus*), and striped killifish (*Fundulus majalis*) (in Neumann et al. 1975) but was not observed in arctic grayling (*Thymallus arcticus*) (McLeay et al. 1983) or in underyearling coho salmon (*O. kisutch*) (Noggle 1978). Rogers (1969) did not report hematocrit levels, but concluded that fish exposed to SS experienced anoxia based on similar surfacing and gulping behavior of fish in SS and in degassed water. Observations of Early Stuart adults exposed to SS did not reveal surfacing or gulping behavior similar to that described as symptomatic of anoxia. Thus, Early Stuart adults exposed to 1 500 mg • L^{-1} fine sediment may have experienced an undiagnosed impairment in gill function, which caused a slight increase in hematocrit but was not severe enough to elicit behavioral symptoms of anoxia. Smolts exposed to fine sediment concentrations more than nine times those experienced by Early Stuart adults did not have elevated hematocrits. However, smolt hematocrits may have returned to normal during the 48-h period these fish were held in sediment-free water prior to sampling. A return to normal hematocrit values in five hours has been demonstrated for rainbow trout (*Salmo gairdneri*) following exposure to hypoxic conditions (Swift and Lloyd 1974).

In the absence of surfacing behavior attributable to anoxia, surfacing of fish exposed to SS may be related to vertical sediment gradients in test vessels. McLeay et al. (1983) suggested that fish surfacing in tests of SS may be seeking lower SS levels associated with surficial water. Thus, sockeye underyearlings and smolts observed at the surface in the tests of SS reported herein may have been seeking lower SS concentrations and not displaying anoxic behavior.

The tolerance of salmonids to SS has been the subject of numerous studies but there is limited information on the particle sizes and angularities of sediments tested. This study demonstrated that LC50 decreased as particle size increased for particles described as angular to subangular. Newcomb and Flagg (1983) report the 36-h LC50 of Mt. St. Helens volcanic ash to be 6 100 mg • L^{-1} for sockeye smolts. On the other hand, as reported herein, no mortalities occurred when sockeye smolts were exposed to 14 407 mg • L^{-1} of Ft. Langley sediments. The volcanic ash is described as having a particle size range from less than 5 to 100 µm with the majority less than 15 µm and the shape was described as angular. Thus, the particle sizes of the volcanic ash were only slightly greater than Ft. Langley sediments. In addition, the volcanic ash was reported composed largely of angular particles while Ft. Langley sediments were angular to subangular. These data suggest that the combination of slightly larger, more angular particles in volcanic ash, compared to Ft. Langley sediment, may have caused the former to be more lethal. However, there were no photographs of the volcanic ash so a direct comparison with Ft. Langley sediments could not be made. Noggle (1978) estimated 96-h LC50 values for wild underyearling coho exposed to Quillayute Prairie soils in August at 1 200 mg • L^{-1} and in excess of 30 000 mg • L^{-1} in November. However, the latter value was based on a test where the SS were about 8 000 mg • L^{-1} for half of the 96-h test period. Sixty-five percent of Quillayute sediments were greater than 50 µm and the particles were described as very angular to angular, based on Blatt et al. (1972). Assuming similar bases for comparing angularity, these data indicate that Quillayute sediments were slightly coarser and more angular than Ft. Langley sediments or Mt. St. Helens volcanic ash. Accordingly, the LC50 of 1 200 mg • L^{-1} reported for underyearling coho fits the trend observed for sockeye wherein tolerance decreased as angularity and particle size increased. The LC50 for coho tested by Noggle (1978) in November may be between 8 000 and 30 000 mg • L^{-1}, but whatever the correct value, tolerance appeared to increase over measurements in August. The increase in tolerance may have been due to acclimation and decrease in temperature as Noggle (1978) suggested. Evidence presented by Sherk et al. (1974) suggests that pre-exposure to SS stimulates proliferation of gill mucous cells and thus may mitigate the effects of SS. Sherk's results lend some credence to Noggle's suggestion concerning acclimation to SS.

Arctic grayling, measuring 7.1 cm, survived four and 16-day exposures to 250 000 and 50 000 mg • L^{-1}, respectively, of placer mining sediments (McLeay et al. 1983). Over 90% of the particles in these test sediments were less than 200 µm while 70 and 60-65% were less than 50 and 38 µm, respectively. Particle angularity was not described. The particle sizes of these sediments were between those of Ft. Langley and Quillayute but were much less toxic to grayling than were the Ft. Langley and Quillayute sediments to coho and sockeye salmon. The lower toxicity to grayling may be due to a combination of factors including differences in species and sediments. It is evident from the foregoing comparisons that further research is needed to describe correlations among particle size, sediment characteristics, and fish species.

Elevation of plasma glucose is considered a secondary stress response in salmonids (Mazeaud et al. 1977). When Early Stuart and Cultus Lake sockeye were exposed to 1 500 and 500 mg • L^{-1} SS, respectively, plasma glucose was elevated 150 and 39%. Arctic grayling responded to 50 mg • L^{-1} of placer mining sediments in a similar manner (McLeay et al. 1983). The outcome of a stress response is dependent on factors such as duration of exposure, temperature, and other environmental variables. In the case of adult Early Stuart sockeye migration in the Fraser River, SS are typically 250 mg • L^{-1} but can average 550 mg • L^{-1} and range as high as 2 500 mg • L^{-1} (unpublished data, IPSFC, Servizi). Travel time of adult Early Stuart sockeye in the Fraser River is about 18 days (Killick 1955). Based on the experimental results, using SS similar to that in the Fraser River, Early Stuart adult sockeye could encounter stress-causing concentrations of SS during spawning migrations.

During smolt migrations, mean SS in the Fraser River at Hell's Gate are typically 600 mg • L^{-1} but can average 1 000 mg • L^{-1} and range as high as 3 000 mg • L^{-1} in a single sample (unpublished data, IPSFC, Servizi). The tests reported herein indicate that SS are unlikely to cause gill injury or acute osmoregulatory stress among Fraser River sockeye smolts in sea water. Underyearling sockeye experienced gill trauma at 3 143 mg • L^{-1} and this level of SS has been measured at Hell's Gate. Small numbers of underyearling sockeye occur in the lower Fraser River near Vancouver and these may be subjected to high levels of SS. Fry and underyearlings of the other four species of Pacific salmon are present in various parts of the Fraser River when SS are high but further studies are required to assess the tolerance of these species to SS.

Conclusions

1. The 96 h LC50's of four Fraser River sediments to underyearling sockeye ranged from 1 674 to 17 560 mg • L^{-1} and were related to particle size.

2. Fine sediment used in tests was typical of suspended sediment in the Fraser River.

3. Gill trauma occurred among underyearling sockeye at 0.18 of the 96-h LC50 of fine sediment.

4. Osmoregulatory capacity of smolts was slightly impaired by exposure to 14 407 mg • L^{-1} fine sediment, but plasma chloride remained below acute stress levels.

5. Adult sockeye displayed a secondary stress response, elevated plasma glucose, following nine and 15-day exposures to 1 500 and 500 mg • L^{-1} of fine sediments.

6. Suspended solids levels as high as those causing a secondary stress response in adult sockeye in the laboratory have occurred in the Fraser River during summer spawning migrations.

7. Comparisons of data reported herein with published reports indicate further study is required to relate tolerance of fish to characteristics of suspended sediments.

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Section II
Fishery Management — Past, Present, and Future
a) The Tools of Management

Evaluation of the Reliability of Several Models Used to Forecast the Size of Adult Sockeye Salmon (*Oncorhynchus nerka*) Runs

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Abstract

HENDERSON, M. A., D. PEACOCK, AND R. GORUK. 1987. Evaluation of the reliability of several models used to forecast the size of adult sockeye salmon (*Oncorhynchus nerka*) runs. p. 266–272. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Several regression models developed to forecast the total size of adult sockeye salmon (*Oncorhynchus nerka*) runs were evaluated on the criteria of minimizing the residual mean square (RMS) based on prediction sum of squares (PRESS). Four types of models were examined: a pre-season model where the forecast return in year *n* equals the average return over the last *n*–1 years (the mean model), a pre-season model developed from historical information on return rates per spawner and the average age structure of returns (the return rate model), four in-season models utilizing various combinations of the variables catch, effort and catch-per-unit-effort, and an in-season model based on the average timing of returning sockeye (the average timing model). The RMS of the mean model was approximately 3.3 times greater than the RMS of the return rate model. The return rate model also had a lower RMS than any of the in-season models through the first 4 wk of a 7-wk fishery. In-season models developed from catch and effort statistics proved to be particularly unreliable for making forecasts of total run size. The implications of these findings for the management of sockeye salmon stocks and fisheries are discussed.

Résumé

HENDERSON, M. A., D. PEACOCK, AND R. GORUK. 1987. Evaluation of the reliability of several models used to forecast the size of adult sockeye salmon (*Oncorhynchus nerka*) runs. p. 266–272. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les auteurs ont évalué plusieurs modèles de régression, mis au point pour prédire la taille totale des remontes de saumon nerka (*Oncorhynchus nerka*) adulte, afin de déterminer lequel minimise la moyenne des carrés résiduelle (RMS) basée sur la prédiction des sommes de carrés (PRESS). Quatre genres de modèles ont été étudiés : un modèle pré-saisonnier où la remonte prévue au cours de l'année *n* est égale à la remonte moyenne au cours des *n*-1 dernières années (le modèle de la moyenne), un modèle pré-saisonnier élaboré à partir des données historiques sur les taux de remonte par géniteur et la composition moyenne par âge des géniteurs amontants (le modèle du taux de remonte), quatre modèle saisonniers portant sur diverses combinaisons des prises, de l'effort et des prises par unité d'effort ainsi qu'un modèle saisonnier basé sur le moment moyen de la remonte des saumons nerkas (le modèle du moment moyen). La RMS du modèle de la moyenne était environ 3.3 fois plus élevée que la RMS du modèle du taux de remonte. De plus, le modèle du taux de remonte montrait une plus faible RMS que tous les modèles saisonniers pendant les 4 premières semaines d'une saison de pêche qui durait 7 semaines. Les modèles saisonniers élaborés à l'aide des statistiques sur les prises et l'effort se sont révélés particulièrement peu sûrs pour l'établissement de prévisions de la taille totale de la remonte. Les auteurs examinent les implications de ces découvertes sur la gestion des stocks et l'exploitation du saumon nerka.

One of the most important tasks of a salmon manager is to forecast the size of stocks returning to their spawning grounds. Generally, two types of forecasts are prepared. Pre-season forecasts are made prior to the start of the fishing season and provide the manager with the first estimate of total run size. The manager can then make some preliminary decisions regarding regulation of various fisheries to achieve target escapements or exploitation rates. The pre-season forecasts are also used by fishermen in making tentative decisions on how they will allocate their effort among various fisheries, at least for the first part of the fishing season. Following the initiation of the fishing season, in-season estimates of abundance are formulated. In-season estimates are generally regarded as more reliable than pre-season estimates (Walters and Buckingham 1975) and are used by both salmon managers and fishermen in re-evaluating their earlier decisions based on pre-season forecasts.

Although many models have been developed to forecast total run size, most rely on only a few variables. Pre-season models generally require historical information on the number of fish returning per spawner and the average age composition of the returning stock. This information is then used to estimate stock abundance based on escapements in appropriate brood years. Most in-season models utilize some combination of weekly catch and effort data from a commercial fishery. Indicators of stock abundance at various times in the fishing season are developed from these data and related to total stock abundance by regression analysis to produce a model suitable for forecasting run size. In addition to catch and effort data, historical information on run timing may also be used in developing in-season models.

Despite the importance of forecasts of total run size to both managers and fishermen, no attempt has been made to systematically evaluate the reliability of the various models commonly used to generate forecasts. The objective of our study is to select from an array of models those that provide the most reliable forecasts of total run size both before and during the fishery. We also show, for 1 wk in 1 yr of a sockeye fishery, the 95% confidence limits on forecasts produced from each model and discuss the management implications at these levels of uncertainty.

Methods

The primary requirement for evaluating models used to forecast total run size for salmon is a stock with a time series of accurate catch and escapement data which, in addition, has shown considerable variation in total run size. The Smith Sound sockeye stock meets these requirements. Smith Sound, which is geographically coincident with the Canadian Department of Fisheries and Oceans Statistical Area 10, is located on the central coast of British Columbia slightly north of Vancouver Island between 51° 10′ and 51° 20′ north latitude (Fig. 1).

Returning spawners approach Smith Sound primarily from the west although in some years a small component may move towards the Sound from the north. During the course of their return migration, no directed fishery occurs on Smith Sound sockeye outside of Smith Sound (English 1983a, 1983b; Leavens and Birch 1984) After moving through Smith Sound, the sockeye pass a counting fence on the Docee River on the way to spawning areas in Canoe and Smokehouse

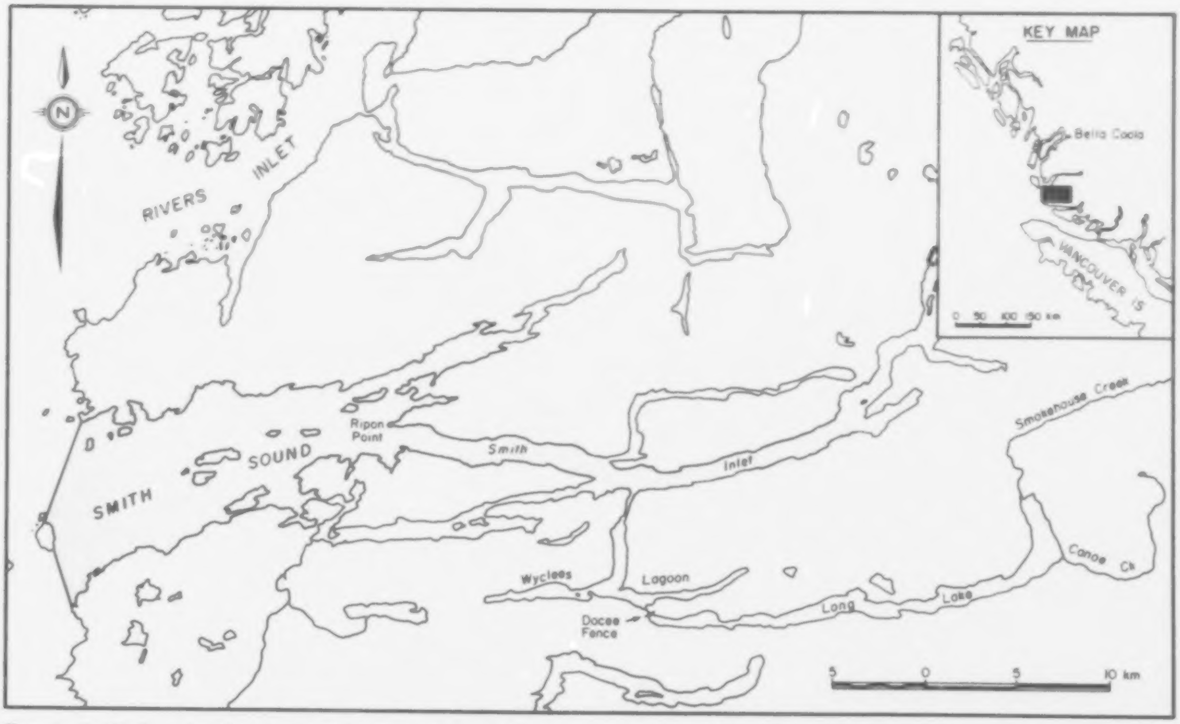

FIG. 1. Smith Sound and vicinity. Shaded area shows the location of the Smith Sound sockeye salmon fishery.

creeks (Fig .1). The fence has been in place since 1972.

In most years between 1972 and 1983, the period of our study, the fishery has been restricted to the area of Smith Sound and Smith Inlet (Fig. 1). In 1973, 1974, 1982, and 1983, however, Wycless Lagoon was open to fishing for short periods of time. Usually over 80% of the total fishing effort is concentrated in the first few kilometres on the western edge of the fishing boundary of Smith Sound. Gillnets are the only gear employed in the Smith Sound fishery. Generally the sockeye fishery commences in late June and may continue as late as early August. The target species of the fishery shifts in late July from sockeye to pink and chum salmon.

There are two independent sources of daily catch and effort data for the Smith Sound fishery. Sales slips containing these data are generated by commercial processors when fishing vessels off-load. Also, hail estimates of total catch, and visual estimates of total effort are made throughout the season by fishery managers. The correlation coefficient when the total annual sockeye catch estimated from sales slips was correlated with the hail estimates between 1972 to 1983 was 0.978. Our analyses were based on the hail estimates of catch and visual estimates of effort. Estimates of escapement at the Docee fence can, for the purposes of our study, be considered to be without error.

Seven models, two pre-season and five in-season, were constructed to forecast total stock size. Six models required regressing total stock size from 1972–83 inclusive on the appropriate X variable(s). The seventh and most reduced regression model, referred to as the mean model, had no measured X variable. The prediction sum of squares (PRESS) (Allen and Cady 1982) was calculated for each model and divided by the appropriate degrees of freedom to produce the residual mean square (RMS). The model producing the smallest RMS for any given time period was then identified as the best model for forecasting total run size. Model coefficients were estimated using the Abbreviated Doolittle algorithm (Allen and Cady 1982).

PRESS is obtained by predicting each observation using all other observations. The resulting residuals are squared and summed to form PRESS. The residual sum of squares (RSS) commonly used in regression analyses are themselves not useful as a criteria for model selection (Allen and Cady 1982). It can be shown that while the RSS decreases as variables are added to a model the variance of a forecast value will not decrease and in general will increase with each additional variable. Also, results obtained from including an observation, y_1, in a regression that is then used in calculating an estimated y_1 would be overly optimistic. Consequently in model selection, there is a trade-off between including variables that will reduce the RSS from the use of an insufficient model and including variables that have little effect on the RSS but will increase the variance of the forecasted value. The PRESS is a more realistic criteria for comparing models and is appealing because it simulates prediction; it does not use an observation to aid in the prediction of itself.

The first pre-season model, the simplest and most reduced of all the models, is of the form:

$$(1) \qquad \hat{y}_i = \bar{y} X_{i0} + \varepsilon_i$$

where $\hat{y}_i$ is the forecast run size for year i, $\bar{y}$ is the arithmetic mean of the total run size for the years 1972 to 1983, $X_{i0} = 1$, and ε_i is the random component. This model, denoted here as the mean model, is not often used to forecast total run size, however, it does serve as a useful basis from which to compare the relative reliability of all other models. Tne structure of the second pre-season model is:

$$(2) \qquad \hat{y}_i = \beta_0 X_{i0} + \beta_1 X_{i1} + \varepsilon_i$$

where X_{i1} is the predicted stock size in year i, β_0 is the intercept, and β_1 is the partial regression coefficient for the X_1 variable. The stock prediction for each year i from 1972 to 1983 was calculated by first determining the average proportion of 4- and 5-yr-old sockeye in the returning stock over this period based on scale samples collected from the fishery and the fence. Next, the total expected return from escapements in years $i-4$ and $i-5$ was estimated by taking the product of the escapement and return rate per spawner. Long Lake, the nursery lake for the Smith Sound sockeye stock (Fig. 1), was fertilized in 1977, 1978, and 1979. The return rate for these brood years was estimated to be 4.0:1.0. For all other years the calculated return rate was 2.5:1.0. The total expected returns from brood years $i-4$ and $i-5$ were then apportioned according to the average age structure of returns which was approximately 35% 4-yr olds and 65% 5-yr olds. Finally, returns for each brood year were summed to produce the predicted run size for year i. This model which is referred to as the return rate model, represents the most common approach to formulating pre-season expectations.

Three of the in-season models, with a similar structure to equation (2), are of the form:

$$(3) \qquad \hat{y}_{ij} = \beta_0 X_{ij0} + \beta_1 X_{ij1} + \varepsilon_{ij}$$

The first model is the weekly catch-per-unit-effort (CUE) model where $\hat{y}_{ij}$ equals the forecast run size in week j of year i, β_0 is the intercept, X_{ij0} equals 1, X_{ij1} is the total sockeye catch divided by the total effort in boat days for successive 7-day periods, j, in year i, β_1 is the partial regression coefficient for X_{ij1} and ε_{ij} equals the random component for week j and year i.

The second in-season model, referred to as the Σ CUE model, is similar except catch and effort data were accumulated over weeks to form X_{ij1} so that, for example, the Σ CUE in week two of a fishery would equal the total catch in the first 2 wk divided by the total effort in the first 2 wk.

The third in-season model with the structure of equation (3) is the average timing model where X_{ij1} is the estimate of total run size for week j in year i. The X_{ij1} values are determined by first generating daily estimates of the proportion of the total run that would have passed through the fence in the absence of a fishery for each year between 1972 and 1983. As it takes sockeye approximately 5 days to move from the fishery to the Docee fence, this is done by combining escapement on day Z with catch on day $Z-5$ and summing it with the estimate of the number of fish that would have passed through the fence in the absence of a fishery up to and including day $Z-1$. We then determine the average proportion of the run to have passed the fence for each day of the fishery over the 1972 to 1983 period. Finally, to arrive at the X_1 value for any date on any given year we take the product of the inverse of the average proportion of the stock to have passed the fence by that day and the total number of sockeye estimated to have passed through the fence by that same day in the absence of a fishery. We will refer to timing and run size estimated assuming no fishery as theoretical timing and theoretical run size.

The fourth in-season model is of the form:

$$(4) \qquad \hat{y}_{ij} = \beta_0 X_{ij0} + \beta_1 X_{ij1} + \beta_2 X_{ij2} + \varepsilon_{ij}$$

This model, referred to as the Σ CUE + Σ E model (E = effort), is the same as the Σ CUE model described above except for the addition of the X_{ij2} variable and its partial regression coefficient β_2. X_{ij2} is cumulative effort up to and including week *j* of year *i*. The structure of the final in-season model is:

$$(5) \qquad \hat{y}_{ij} = \beta_0 X_{ij0} + \beta_1 X_{ij1} + \beta_2 X_{ij2} + \beta_3 X_{ij3} + \varepsilon_{ij}$$

This is the Σ CUE − Σ E − Σ C model (C = catch) and is the same as the model described in equation (4) except for the addition of X_{ij3} and its partial regression coefficient β_3. X_{ij3} is the cumulative catch up to and including week *j* of year *i*. Only weeks when 25 or more boats operated in the fishery were used in the analyses. This rule occasionally excluded the first week of the fishery from the analysis.

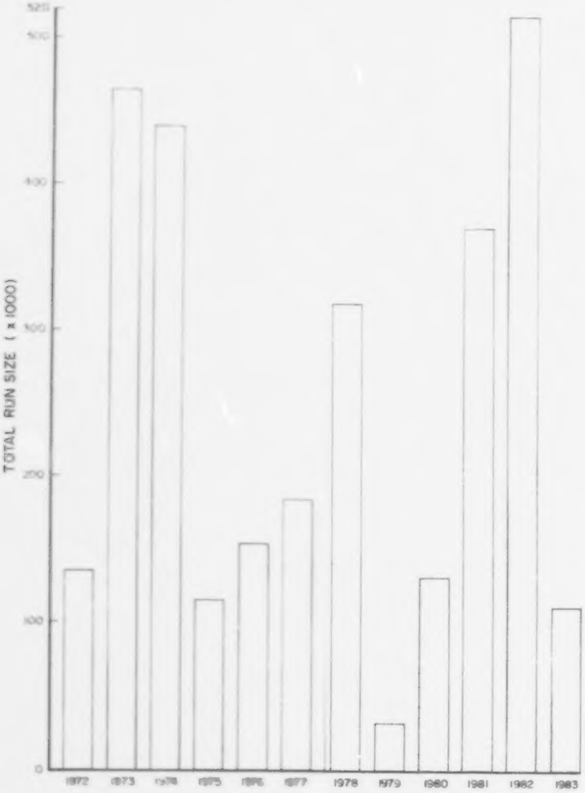

FIG. 2. Total run size (catch plus escapement) for Smith Sound sockeye salmon from 1972 to 1983.

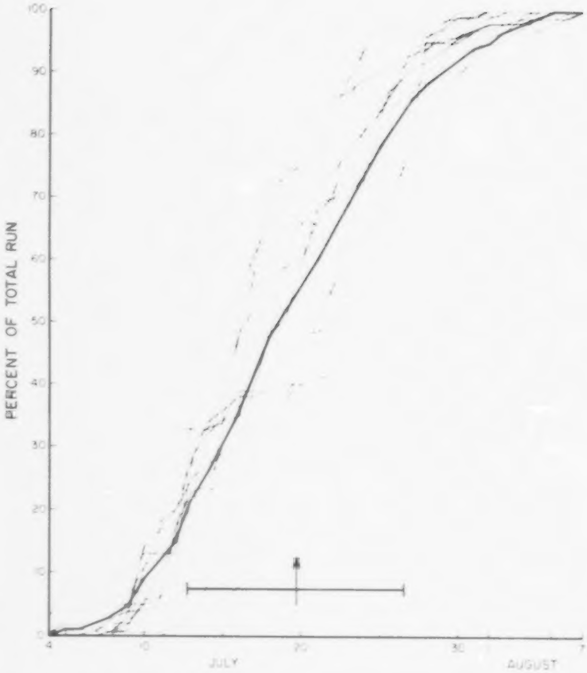

FIG. 3. Percent of the total Smith Sound sockeye salmon run returned by date for 1972 to 1983 (thin lines) and average percent of the total run returned by date for 1972 to 1983 (heavy line). Total returns for day *Z* equal the count at the Docee fence on day *Z* plus the catch in the Smith Sound fishery on day *Z*−5 (see text for details). Arrow indicates the day when, on average, the percent of the total run first equals or exceeds 50%. The horizontal line shows the 95% confidence limit.

Results

The size of the Smith Sound sockeye stock (catch plus escapement) varied by more than an order of magnitude during the 12 yr examined in our study from a low of approximately 30 thousand in 1979 to over 500 thousand in 1982 (Fig. 2). The average total run size was 266 thousand sockeye. Escapement exhibited similar variation ranging from 21 thousand to 214 thousand and averaging 111 thousand. The theoretical run timing measured at the Docee fence also exhibited considerable variation between years (Fig. 3). Smith Sound sockeye were detected in the fishery as early as June 25 and passed through the fence as late as August 6. On average from 1972 to 1983, 50% of the total theoretical run had passed the fence by July 19. The actual dates when 50% of the total theoretical run passed the fence ranged from July 15 in 1980 to July 28 in 1979.

The intercepts and partial regression coefficients for the models used to forecast total run size are shown in Table 1. All partial regression coefficients were large enough to indicate that each of the *X* variables can account for an important part of the variability in total run size. The intercept for the mean model, 265910, is equal to the average total Smith Sound sockeye run size from 1972 to 1983. The intercept for the return rate model was less than half that of the mean model while the partial regression coefficient, β_1, indicated that on average from 1972 to 1983 the run size

TABLE 1. Intercepts (β_0) and partial regression coefficient (β_1, β_2, and β_3) for models used to forecast stock abundance.

	Model						
	Mean	Return rate	Weekly CUE	Σ CUE	Σ CUE + Σ Effort	Σ CUE + Σ · Effort + Σ Catch	Average timing
June 30							
β_0	265 910	123 780	179 504	179 504	219 170	−268 401	
β_1		1.38	2 831.39	2 831.39	3 712.00	29 616.32	
β_2					−524.11	3 435.69	
β_3						−144.15	
July 7							
β_0	265 910	123 780	111 583	100 695	−33 839	−125 801	224 680
β_1		1.38	2 650.08	2 748.40	3 068.26	4 336.97	3.62
β_2					298.91	632.48	
β_3						−5.38	
July 14							
β_0	265 910	123 780	128 841	58 738	−11 435	−64 804	174 574
β_1		1.38	1 927.75	3 175.06	3 074.69	4 038.09	0.28
β_2					88.74	156.49	
β_3						−1.18	
July 21							
β_0	265 910	123 780	199 213	132 297	38 848	−57 137	67 784
β_1		1.38	959.49	1 769.41	1 552.11	2 182.63	0.75
β_2					82.31	124.86	
β_3						−0.13	
July 28							
β_0	265 910	123 780	191 632	128 855	16 181	55 262	8 207
β_1		1.38	1 464.12	1 805.26	1 622.61	626.10	0.96
β_2					83.72	35.68	
β_3						0.91	
Agust 4							
β_0	265 910	123 780	97 787	122 766	14 953	47 504	186
β_1		1.38	3 563.04	1 903.14	1 596.16	834.47	0.97
β_2					82.25	43.75	
β_3						0.71	
August 11							
β_0	265 910	123 780	308 461	121 022	3 970	41 699	0
β_1		1.38	−2 172.14	1 942.72	1 745.21	905.26	1.00
β_2					81.91	46.16	
β_3						0.67	

forecast from the return rate model underestimated the actual run size. The magnitude of the partial regression coefficients for the weekly CUE model were approximately inversely related to the corresponding weekly estimates of CUE, declining from late June through mid-July then increasing after most of the run had passed through the fishery. The intercepts for the three in-season models , employing one or more of the variables Σ CUE, Σ E, and Σ C, decreased from very large values early in the fishery to smaller, relatively stable values by mid-July. In all weeks after mid-July the absolute value of the intercept in the Σ CUE model was much larger than in the other two. In turn the intercepts for the weekly CUE model were larger than those for the Σ CUE model in all but one week after June 30. The partial regression coefficients, B_1, β_2, and β_3, for the three models also stabilized after the middle of July. The apparent stability in the intercepts and partial regression coefficients resulted because most of the catch and effort had occurred by then. The intercept for the average timing model decreased continuously over the period of the fishery to a value of zero with a corresponding β_1 value of 1.0 on Agust 11 indicating that all sockeye in the Smith Sound stock have been accounted for by this date.

The RMS was lowest for the return rate model from the beginning of the fishery through the week ending July 21 indicating this is the most reliable model for forecasting sockeye run size over this period (Fig. 4). The RMS for the mean model was more than three times greater than the RMS for the return rate model. The RMS for the three in-season models using various combination of Σ CUE, Σ E, and Σ C decreased from very high values early in the fishery to levels that remained approximately stable after July 28. The RMS of these three models were generally greater than the RMS for the mean model through July 14 and in only one instance during the entire period examined, on July 28 for the Σ CUE + Σ E model, was the RMS of any of these models less than that estimated for the return rate model. The RMS for the weekly CUE model exhibited a similar trend declining discontinuously through August 4. The average timing model showed a precipitous decrease in its RMS but again, as in the other models, it did not decrease below the RMS of the return rate model until late in the fishing season.

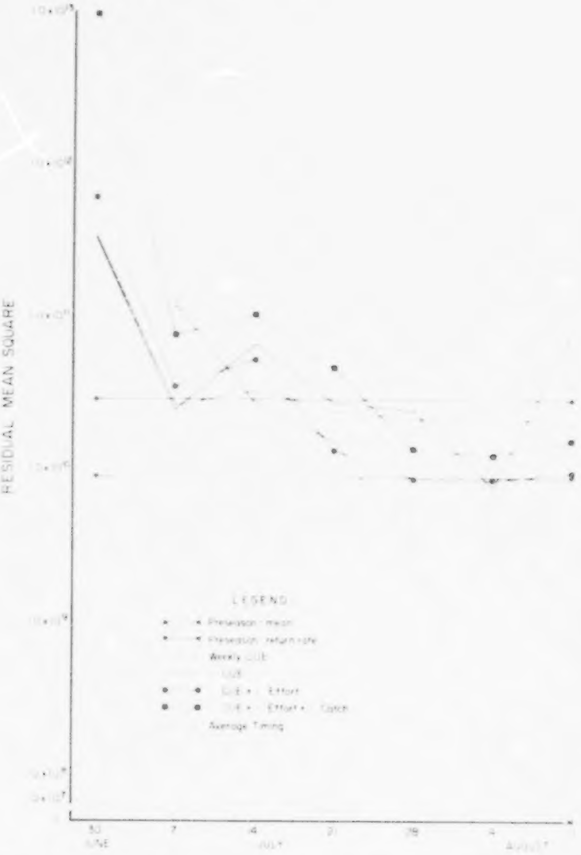

FIG. 4. Residual mean square associated with models used to forecast run size prior to the start of the fishery and at weekly intervals during the fishery.

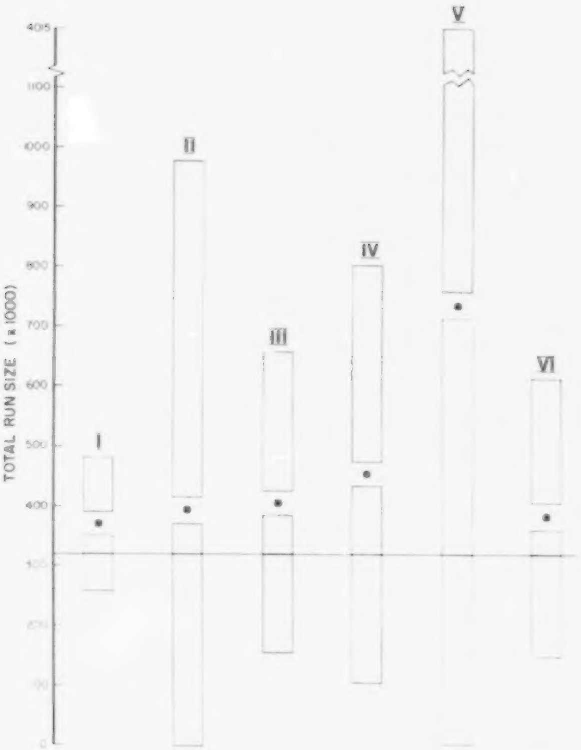

FIG. 5. Forecast total run size (●) made on July 14 for the 1978 return using model I = return rate model, II = weekly CUE model, III = Σ CUE model, IV = Σ CUE + Σ Effort model, V = Σ CUE + Σ Effort + Σ Catch model and VI = average timing model. Vertical bars show the 95% confidence limits. Horizontal line is the actual total run size in 1978.

The degree of uncertainty in forecasts generated by the models described above is proportional to their respective RMS. For example, in the week ending July 14, 1978 the 95% confidence limits on the forecast total run size using the return rate model were 257 thousand and 482 thousand (Fig. 5). The actual total run size in 1978 was 318 376 sockeye. The 95% confidence limits for the weekly CUE model were much larger ranging from 0 to almost one million. 95% confidence limits for models employing combinations of Σ CUE, Σ E, and Σ C increased with each additional variable from 154 thousand to 657 thousand for the Σ CUE model to 0 to over four million for the Σ CUE + ΣE + Σ C model. The same limits for the average timing model were 150 thousand to 617 thousand.

Discussion

Two very important observations pertinent to the management of sockeye salmon stocks emerge from our study. The first is the apparent reliability of the pre-season return rate model. This model, constructed from historical information on the number of fish returning per spawner and the age composition of returns, provides the most reliable forecasts of total run size through all but the last 3 wk of the fishing season (Fig. 4). In addition, these forecasts can be made almost 4 yr prior to the fishery allowing managers ample time to make any necessary changes to the fishery to achieve desired exploitation rates or escapements. The second important observation relates to the large degree of uncertainty in forecasts made from models using catch and effort statistics from the commercial fishery. The RMS of all four models, weekly CUE, Σ CUE, Σ CUE + ΣE, and Σ CUE + Σ E + Σ C, exceeds that of the return rate model throughout most of the fishery. In fact, the RMS of these models generally exceeds the RMS of the mean model during the first half of the fishery. This is a particularly serious problem as it is in the initial weeks of the fishery when the most crucial decisions must be made to achieve management goals. In that sense the reduction in the RMS in the latter part of the fishery, particularly in the Σ CUE + Σ E and Σ CUE + Σ E + Σ C models, to where they approach the RMS of the return rate model is of little consequence.

There are several limitations with the approach to forecasting used in our study. While regression models were developed for making forecasts, the X variables were not truly independent. Consequently, while unbiased forecasts can be made, they can only be made over the range of historical conditions (e.g. run sizes) used for estimating the intercepts and partial regression coefficients of the models.

Forecasts developed from data lying outside this range are subject to a larger but undefined level of uncertainty.

All models examined in our study required estimates of catch and escapement. The reliability of forecasts from these models will therefore depend in part on the accuracy of the catch and effort statistics. The Smith Sound sockeye stock and fishery probably represents a near optimal situation. The fishery is small with well defined boundaries and the stock is not known to be intercepted in other fisheries. In addition, all escapement of the stock is measured at the Docee fence. A more typical situation in British Columbia is for a stock to be intercepted in several fisheries, the boundaries and intensity of which change from year to year. In addition, escapement estimates for most stocks are made by foot or aerial surveys which are known to have a high level of sampling error (Walters and Ludwig 1981; Cousens et al. 1982; Symons and Waldichuk 1984). The increased uncertainty in both catch and escapement statistics will result in less reliable forecasts of total run size than those described in our study.

There is one additional difficulty associated with the models using catch and effort statistics. Generally, when the Smith Sound sockeye run is forecast to be small there is either a very short fishery or no fishery at all. This situation would persist until such time as there was an indication that the run was actually not as small as expected. Consequently, very little catch and effort information is available for small stock sizes and as a result the forecasts for small run size using the models described in our study are not reliable.

We have shown an absolute level of uncertainty associated with forecasts generated from each model during the middle portion of the 1978 Smith Sound fishery (Fig. 5). The amount of uncertainty and hence the risk of relying on these forecasts or forecasts for any other week or year are directly proportional to the chosen α level. In our example we rather arbitrarily chose an α level of 0.05. Whether a manager really requires that the final run size falls within the confidence limits of his forecast 19 times out of 20 is problematic. Certainly the confidence limits can be reduced by choosing a larger α level. For example the 95% confidence limits for the Σ CUE model made on July 14, 1978 extended from 154 000 to 657 000 sockeye (Fig. 5). If we adopted 60% confidence limits ($\alpha = 0.40$) the range for the same forecast would be 193 000 to 591 000. Ultimately the choice of an α level is going to be stock specific and depend on several factors including the perceived social and economic value of the stock, and the health of the stock. The relative degree of uncertainty in forecasts based upon the various models will not change, however, as it depends on the RMS for each model and the risk that the manager is willing to take that the forecast will be wrong.

The estimates of RMS for all models evaluated in our study were rather large (Fig. 4). However, for the Smith Sound sockeye stock and fishery the RMS and confidence limits on forecasts of total run size using the return rate model are small enough to be useful for the management of the stock. This indicates that, contrary to more common belief, preseason forecasts can be useful for in-season management. The usefulness of the return rate model, however, is entirely dependent on having accurate escapement estimates. This suggests that we should devote a considerable amount of our resources and effort over the next few years to developing systems that produce accurate, absolute escapement estimates for as many sockeye stocks as possible. In conjunction, for most stocks, we require better estimates of interception rates in non-terminal fisheries so that we develop more reasonable estimates of total catch and therefore total run size. Under these conditions reliable pre-season models similar to the return rate model described here could be developed. In the longer term pre-season models could be further improved if we begin to gather quantitative information on factors affecting ocean survival.

None of the models employing catch and effort statistics appear useful for forecasting total run size of the Smith Sound sockeye stock. It should be emphasized that all catch and effort data were obtained from the commercial fishery. This in itself presents problems as the fishing power and consequently catchability coefficient of fishing vessels changes with time as do the boundaries of fisheries and the actual behavior of fish stocks. This suggests that a test fishery, fishing with a fixed type of gear in standard locations every year for the duration of the "normal" commercial fishery, would produce lower RMS values. Although we believe this to be true, we think it is unlikely that the RMS of models based on catch and effort statistics can be reduced sufficiently so that they could become the preferred in-season forecasting models. This is particularly true during the first part of the fishing season when final management decisions must be made to achieve target exploitation rates or escapements.

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Forecasting Sockeye Salmon (*Oncorhynchus nerka*) Returns to Bristol Bay, Alaska: A Review and Critique of Methods

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Abstract

FRIED, S. M., AND H. J. YUEN. 1987. Forecasting sockeye salmon (*Oncorhynchus nerka*) returns to Bristol Bay, Alaska: a review and critique of methods, p. 273-279. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Preseason forecasts of numbers of sockeye salmon returning to Bristol Bay are made by Alaska Department of Fish and Game (ADFG) for nine individual river systems as well as for all of Bristol Bay. Since annual returns of sockeye salmon to Bristol Bay have varied greatly (from about three million to over 65 million sockeye salmon), accurate forecasts are important to ADFG and the fishing industry for preseason planning. Forecasts prepared by ADFG investigators during the last 26 yr (1961-86) have been within about 45% of actual returns. We compared results from different forecasting methods for 6 yr (1981-86) for all of Bristol Bay and for 7 yr (1980-86) for the Kvichak River system to determine which method was most accurate. Japanese Research Vessel (JRVC) method hindcasts, made by using Japanese research vessel catch data along with air temperature data in a multiple linear regression model, were only slightly more accurate than Standard ADFG method forecasts for all of Bristol Bay, made by averaging results from separate linear regression models for spawner-recruit, sibling, and smolt data for all river systems. For the Kvichak River, linear regression model forecasts based on smolt data were generally more accurate than linear regression models based on either spawner-recruit or sibling data. Pooled estimates from several different analytical methods generally resulted in more accurate forecasts than were produced by any of the individual methods. The models and pooling methods presented in this paper should make possible total Bristol Bay and individual river system forecasts which, on average, will be within about 20 and 50%, respectively, of actual sockeye salmon returns.

Résumé

FRIED, S. M., AND H. J. YUEN. 1987. Forecasting sockeye salmon (*Oncorhynchus nerka*) returns to Bristol Bay, Alaska: a review and critique of methods, p. 273-279. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Des chercheurs du ministère de la Chasse et de la Pêche de l'Alaska fournissent des prévisions présaisonnières du nombre de saumons nerkas amontants dans la baie Bristol en direction de neuf systèmes fluviaux ainsi que pour l'ensemble de la baie Bristol. Comme les remontes annuelles de saumons nerkas dans la baie Bristol ont fortement varié (d'environ trois millions à plus de 65 millions de saumons nerkas), des prévisions précises sont importantes pour la planification pré-saisonnière effectuée par le ministère et l'industrie halieutique. Les prévisions calculées par les chercheurs du ministère au cours des 26 dernières années (1961-1986) se sont situées aux environs de 45 % des remontes réelles. Les auteurs comparent les résultats fournis par différentes méthodes de prévision pour 6 années consécutives (1981-1986) pour l'ensemble de la baie Bristol et pour 7 années consécutives (1980-1986) pour le système de la rivière Kvichak afin de déterminer quelle méthode était la plus précise. Des prévisions a posteriori selon la méthode utilisée par les navires de recherche japonais, obtenues d'un modèle de régression linéaire multiple portant sur les données des captures réalisées par les navires de recherche japonais et les données sur la température atmosphérique, étaient légèrement plus précises que les prévisions obtenues avec la méthode normalisée du ministère pour l'ensemble de la baie Bristol. Ces prévisions sont la moyenne des résultats obtenus de différents modèles de régression linéaire des données sur les géniteurs-recrues, la progéniture et les smolts recueillies dans tous les systèmes fluviaux. Pour ce qui est de la rivière Kvichak, des prévisions basées sur un modèle de régression linéaire des données sur les smolts étaient généralement plus précises que des modèles de régression linéaire basés soit sur des données sur les géniteurs-recrues ou la progéniture. Un regroupement des estimations obtenues de plusieurs méthodes analytiques a généralement donné des prévisions plus précises que celles fournies par chaque méthode. Les modèles et les méthodes de regroupement présentés dans ce document devraient permettre des prévisions pour l'ensemble de la baie Bristol et pour chaque système fluvial, qui se rapprocheront, en moyenne, de 20 et 50 % respectivement des remontes réelles de saumon nerka.

Introduction

River systems in Bristol Bay, Alaska, produce about half of the sockeye salmon (*Oncorhynchus nerka*) harvested in North America (Fredin 1980). Total annual returns have ranged from about three million to 65 million sockeye salmon (Fig. 1). Although some sockeye salmon are harvested on the high seas, primarily by Japanese fishing vessels (Fredin et al. 1977), most are caught within 3 miles of the Alaskan shore. The State of Alaska, Department of Fish and Game (ADFG), controls the domestic inshore harvest to ensure that adequate numbers of sockeye salmon escape into each river system to spawn. When commercial fisheries occur in areas where salmon stocks intermingle, it is very difficult to achieve allowable harvest levels for individual spawning stocks, so most commercial fishing effort for Bristol Bay sockeye salmon is restricted to five fishing districts (Naknek–Kvichak, Egegik, Ugashik, Nushagak, and Togiak) located in the vicinity of major spawning systems. Although some harvest of returning Bristol Bay sockeye salmon is allowed along the south side of the Alaska Peninsula (South Unimak) and near the Shumagin Islands, these catches have been limited by a quota system since 1978.

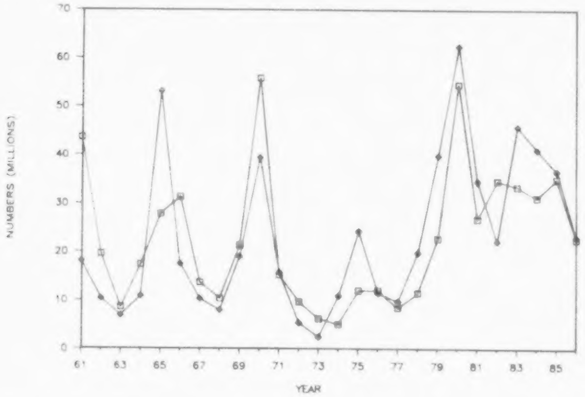

FIG. 1. Actual (◇) and forecasted (□) numbers of sockeye salmon returning to Bristol Bay, Alaska, 1961–86. Forecasted numbers for 1961–82 were based on Standard Alaska Department of Fish and Game (ADFG) method results. Forecasted numbers for 1983–86 were based on the weighted mean of Standard ADFG results and those of other methods described in the text.

Preseason forecasts of sockeye salmon returns are made by ADFG staff for nine individual river–lake systems (Kvichak, Naknek, Branch, Egegik, Ugashik, Nuyakuk, Wood, Igushik, and Togiak) as well as for all Bristol Bay systems combined. These forecasts are used by ADFG staff to estimate commercial harvests; to set quotas for interception fisheries; and to determine which stocks might be in low abundance and need protection against possible overharvesting. Seafood buyers and processors use forecasts to estimate the supply of raw fish which will be available for various uses; to determine staff and equipment needed for production of fresh, frozen, and canned products; and to plan deployment of tenders and processing vessels. Commercial fishermen use forecasts to decide which areas might provide them with the best fishing opportunities and to assist in decisions involving future investments for equipment and gear.

Mathews (1961), using simulation models, showed that use of a preseason forecast with an error of plus or minus 50%, could at that time probably increase the canning industry's seasonal mean operating margin (i.e., the difference between total wholesale value of product and operating costs) by about 13% (from $4.6 million to $5.2 million). He felt that greatest future economic gains would result from improving the accuracy of individual system forecasts, rather than of the total Bristol Bay forecast.

Until 1983, annual preseason forecasts made by ADFG were usually calculated as the mean of predictions obtained from three different data sources: (1) spawner-recruit relationships, (2) sibling returns, and (3) smolt abundance (e.g., Yuen 1982). Forecasts from these data, referred to as Standard ADFG method forecasts, approximated sockeye salmon abundance trends fairly well (Fig. 1) and had a 26 yr (1961–86) mean absolute error within 45% (range, 1–158%) of actual total run size. Attempts have also been made to use other data sources to forecast Bristol Bay sockeye salmon returns. From 1969 until 1979, biologists from the University of Washington (UW) prepared forecasts using numbers of immature sockeye salmon caught by chartered purse seine vessels fishing south of the Aleutian Island of Adak (Harris and Rogers 1979). Since 1982, biologists from ADFG and UW have prepared forecasts using catches of immature sockeye salmon made from Japanese research gill net vessels fishing south of the Aleutians, referred to as Japanese Research Vessel Catches method forecasts (JRVC). However, these forecasts did not provide predictions for individual river systems and their accuracy was similar to that of Standard ADFG forecasts.

Beginning in 1983, ADFG staff attempted to improve forecast accuracy by pooling results of the Standard ADFG method with those of other methods (Eggers et al. 1983a, b). Since 1985, only results of the Standard ADFG and JRVC methods were used within the pooled forecast (Fried and Yuen 1985, 1986).

The purpose of this report is to provide a review and critique of methods used by ADFG to forecast sockeye salmon returns to Bristol Bay, Alaska. Specific objectives are to (1) describe models currently used to forecast total sockeye salmon returns to all of Bristol Bay and to the Kvichak River system, which often has accounted for about 50% of the total annual return; and (2) determine whether forecast accuracy can be improved by pooling results of individual models and methods.

Methods

AGE DESIGNATION

Adult ages were expressed according to Gilbert and Rich (1927) designations, wherein both total age, dated from the time of egg deposition, and year of life in which seaward migration occurred (subscript) are indicated. Four age-classes account for about 98% of total returns: 4_2, 5_3, 5_2, and 6_3 (i.e. sockeye salmon approaching their fourth, fifth, and sixth year of life which migrated seaward in either their second or third year). These four ages-classes were equivalent to the following modified European system designations (Koo 1962): 1.2, 2.2, 1.3, and 2.3, respectively. The number of annular scale checks formed in fresh and salt water are indicated to the left and right of the period, respectively.

Smolt ages were expressed as either age I or II, corresponding to sockeye salmon that migrated seaward in either their second or third year of life, respectively.

Forecasting Models

Standard ADFG — The Standard ADFG method has been used from 1961 to the present to produce individual forecasts, by major age-class, for nine river systems that account for about 98% of Bristol Bay sockeye salmon production: Kvichak, Branch, Naknek, Egegik, Ugashik, Wood, Igushik, Nuyakuk, and Togiak. Forecasts for each age-class were calculated for each river system by averaging results of several models which used either spawner-recruit, sibling, or smolt data. Beginning in 1986, only linear regression models were used to calculate forecasts (Fried and Yuen 1986).

Forecasts from spawner-recruit data were based on a linear form of the Ricker (1954) curve constructed for age-specific returns (Brannian et al. 1982):

$$\ln|R_{i,\,k,\,y} / E_{k,\,y}| = \ln|a| - bE_{k,\,y}, \text{ where}$$

$R_{i,\,k,\,y}$ = number of age i sockeye salmon returning to river system k from spawning during brood year y; $E_{k,\,y}$ = total number of spawners in river system k during brood year y; a and b = parameters which determine the intercept and slope of the line, respectively.

In cases where spawning escapements were much greater (or much less) than any previously observed, predictions for age 4_2 sockeye salmon could not be calculated from spawner-recruit models. However, predictions for ages 5_3, 5_2, and 6_3 sockeye salmon were calculated using the following equations:

$$R_{5,\,k,\,y} = RA_{4,\,k,\,y} / M_{4,\,k}, \text{ where}$$

$R_{5,\,k,\,y}$ = number of 5_2 and 5_3 sockeye salmon expected to return to river system k from brood year y; $RA_{4,\,k,\,y}$ = actual return of 4_2 sockeye salmon to river system k from brood year y; $M_{4,\,k}$ = mean proportion of 4_2 sockeye salmon within past returns to river system k; and

$$R_{6,\,k,\,y} = RA_{4\,\&\,5,\,k,\,y} / (1 - M_{6,\,k}), \text{ where}$$

$R_{6,\,k,\,y}$ = number of 6_3 sockeye salmon expected to return to river system k from brood year y; $RA_{4\,\&\,5,\,k,\,y}$ = actual return of 4_2, 5_3, and 5_2 sockeye salmon to river system k from brood year y; and $M_{6,\,k}$ = mean proportion of $6_{3,\,k}$ sockeye salmon within past returns to river system k.

Forecasts from sibling and smolt data were based upon models using natural logarithm transformed data, as suggested by Peterman (1981, 1982a, b):

$$\ln|R_{i,\,k,\,y}| = a + b\ln|S_{j,\,k,\,y}|, \text{ where}$$

$S_{j,\,k,\,y}$ = *number of age j* (where $j = i$-1) sockeye salmon that returned system k from brood year y; or $S_{j,\,k,\,y}$ = number of age j (where j = age I or II) smolt produced by brood year y and migrating seaward from river system k.

Forecasts for 4_2 and 5_3 sockeye salmon often cannot be made using sibling data, since 3_2 and 4_3 sockeye salmon (i.e. jacks) do not always appear in catch and escapement samples.

Forecasts using smolt data were only made from Kvichak and Wood River systems, where smolt enumeration programs using sonar equipment were begun in 1971 and 1975, respectively. Smolt enumeration programs have recently been started on other systems (Naknek and Egegik in 1982; Ugashik and Nuyakuk in 1983), but sufficient data for fitting models will not be available for several more years.

Japanese Research Vessel Catches — Beginning in 1983, data collected by Japanese research vessels fishing south of the Aleutian Islands during July (e.g. Takagi and Ito 1984) were used in several models, along with Bristol Bay air temperatures (Climatological Data publications, U.S. Department of Commerce, National Climatic Data Center, Asheville, North Carolina), to forecast total returns of sockeye salmon which had remained at sea for either 2 yr (4_2 and 5_3) or 3 yr (5_2 and 6_3) (hereafter referred to as two- and three-ocean age sockeye salmon), respectively (Eggers et al. 1983a, b). In 1985 these data were incorporated into one forecasting model for each ocean age (Fried and Yuen 1985). For the present study, models were also developed for each of the four major age-classes:

$$R_{o,\,z} = a + b_1 G_{(o-1),\,(z-1)} + b_2 L_{(o-1),\,(z-1)} + b_3 C_{(z-1)\,\&\,(z-2)},$$

where $R_{o,\,z}$ = total number of age-group o sockeye salmon returning in year z; $G_{(o-1),\,(z-1)}$ = geometric mean catch per unit of effort of age-group (o-1) in year (z-1); $L_{(o-1),\,(z-1)}$ = mean fork length (mm) of ocean age-group (o-1) in year (z-1); and $C_{(z-1)\,\&\,(z-2)}$ = mean June air temperature at Cold Bay (°F) during year (z-1) for sockeye salmon returning after 2 yr at sea, or the sum of both mean June air temperatures during years (z-1) and (z-2) for sockeye salmon returning after three years at sea.

Comparing Different Forecasting Methods

Four measures of forecast accuracy were used to compare results from different models and methods: (1) annual percent error, (2) mean percent error (MPE), (3) mean absolute percent error (MAPE), and (4) standard error of the regression of forecasted (independent variable) versus actual (independent variable) returns (SE).

Annual percent error values were calculated as:

$$|(A_i - F_i) / A_i| \times 100, \text{ where}$$

A_i = actual return for year i; F_i = forecasted return for year i. Bar graphs were made to assist examination of the distribution and range of positive (underforecasting) and negative (overforecasting) percent errors. MPE, the mean of annual percent error values, was used to examine systematic error (bias) of different forecasting methods. MAPE, the mean of absolute percent error values, was used to examine overall error, since under- and over-forecasting errors were treated similarly. SE (Snedecor and Cochran

1969) was used to measure differences in past returns not accounted for by expected variations due to forecasting methods:

$$\mathrm{SE} = \sqrt{1/(n-2) \sum_{i=1}^{n} (A_i - \hat{A}_i)^2}, \text{ where}$$

$\hat{A}$ = predicted return based on regression of past forecasts on actual returns. Unlike MPE and MAPE, SE provided a measure of forecast error variance and has been used to calculate confidence intervals for forecast estimates (Eggers et al. 1983a, b; Fried and Yuen 1985, 1986). The method with the smallest SE value would, therefore, produce forecast estimates with the narrowest confidence intervals.

Results from separate forecasting models were pooled by calculating either the mean or the weighted mean of individual predictions. SE has been used by ADFG staff since 1983 as the weighting factor for pooling results (Eggers et al. 1983a, b; Fried and Yuen 1985, 1986):

$$F_o = \sum_{m=1}^{2} |F_{o,m} \times (1/\mathrm{SE}_{o,m}^2)| \;/\; \sum_{m=1}^{2} (1/\mathrm{SE}_{o,m}^2), \text{ where}$$

F_o = weighted mean forecast of returns for age-group o; $F_{o,m}$ = forecast of returns for age-group o from method m; $\mathrm{SE}_{o,m}^2$ = forecast standard error squared (variance) of returns for age-group o from method m.

For the present study, mean and weighted mean forecasts of total sockeye salmon returns were calculated for (1) all of Bristol Bay, using previously published Standard ADFG forecasts (Fried and Yuen 1986) and newly calculated JRVC hindcasts, and for (2) the Kvichak River system, using spawner-recruit, sibling, and smolt model hindcasts. Hindcasts were made for each year using models based only on data from previous years.

Comparisons of results from different forecasting methods were made for 6 yr (1981–86) for all of Bristol Bay and for 7 yr (1980–86) for the Kvichak River system. The years which could be examined were limited by data availability and the need for a minimum of 3 yr of results to calculate SE values for use as weighting factors (Snedecor and Cochran 1969). The earliest year for which JRVC model forecasts could be calculated was 1978; the earliest year for which smolt model forecasts for all age-classes could be calculated for the Kvichak River system was 1977.

For all of Bristol Bay, total sockeye salmon return estimates for the following methods were compared: (1) previously published ADFG method forecasts (summarized in Fried and Yuen 1986), which contained results of some models that are no longer used, (2) JRVC hindcasts using separate ocean age models (JRVC-O), (3) JRVC hindcasts using separate major age-class models (JRVC-M), (4) the mean and weighted mean of ADFG and JRVC-O model results, (5) the mean and weighted mean of ADFG and JRVC - M model results, and (6) previously published forecasts (summarized by Fried and Yuen 1986) used by ADFG for past years (1981 and 1982, based only on Standard ADFG results; 1983–85, based on weighted mean of Standard ADFG and some methods that are no longer used).

For the Kvichak River system, total sockeye salmon estimates for the following methods were compared: (1) spawner-recruit model, (2) sibling model, (3) smolt model, (4) the mean and weighted mean of results from all three models, and (5) previously published forecasts (Nelson et al. 1981, 1982, 1983; Eggers et al. 1983a, b; Fried and Yuen 1985, 1986) used by ADFG in past years which contained results of some models that are no longer used.

Results

TOTAL BRISTOL BAY

The JRVC-M method generally performed slightly better than either the Standard ADFG or JRVC-O methods in forecasting total sockeye salmon returns to all of Bristol Bay for 1981–86. The JRVC-M method had a lower MAPE value than either of the other two methods, lower absolute percent errors for 3 of the 6 yr examined, and an equal number of overforecasting and underforecasting errors (Table 1 and Fig. 2). However, the Standard ADFG method had a much lower SE value, and its MAPE value was not very much greater than either of the JRVC methods. The JRVC-O method had a much lower MPE value than either of the other methods, but this was because its tendency to overforecast returns (for 4 of the 6 yr examined) was counteracted by a very large underforecasting error in 1984.

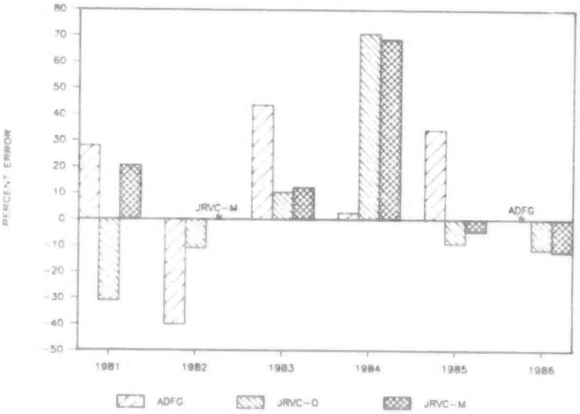

FIG. 2. Percent errors of three methods used to forecast numbers of sockeye salmon returning to Bristol Bay, Alaska, 1981–86. ADFG = previously published Standard Alaska Department of Fish and Game forecasts based on spawner-recruit, sibling, and smolt data (sum of individual forecasts of four major age-classes for nine river systems); JRVC-0 = Hindcasts of returns based on Japanese research vessel catches of immature sockeye salmon (sum of individual hindcasts of two and three-ocean age-classes for all of Bristol Bay); JRVC-M = Hindcasts of returns based on Japanese research vessel catches (sum of individual hindcasts of four major age-classes for all of Bristol Bay).

Pooling results of the Standard ADFG method with either of the JRVC methods (by calculating means or weighted means) resulted in forecasts with lower SE values than any of the component methods and with MPE and MAPE values that were either lower than or intermediate to those of the component methods (Table 1). Performance of the mean and weighted mean of forecast methods was similar. The mean of JRVC-O and Standard ADFG method results produced forecasts with lower MPE and MAPE values, and lower ab-

TABLE 1. Performance of three methods of forecasting total sockeye salmon returns to Bristol Bay, Alaska, 1981–86. (MPE = mean percent error, MAPE = mean absolute percent error, SE = standard error of regression), the most accurate forecast method value is underlined. Forecast methods are explained in the text.

Performance measure	Forecast method			Mean		Weighted mean[a]		Published forecast
	ADFG (1)	JRVC-O (2)	JRVC-M (3)	1+2	1+3	1+2	1+3	
MPE	11.4	3.1	14.2	7.3	28.7	9.5	14.2	9.9
MAPE	24.8	24.0	19.7	18.2	21.5	23.4	25.1	23.3
SE	7.6	14.7	11.3	4.8	3.1	3.8	4.3	5.1

[a] Weighting factor used each year was regression variance for forecasted (independent variable) versus actual returns (dependent variable), for all years prior to, but not including, the year of interest.

solute percent errors for 4 out of the 6 yr examined, than the weighted mean of these methods, although the weighted mean had a slightly lower SE value (Table 1 and Fig. 3). The mean of JRVC-M and Standard ADFG method results produced forecasts with lower MAPE and SE values than the weighted mean of these methods. However, the weighted mean had a lower MPE value and lower absolute percent errors for 5 of the 6 yr examined.

Performance of previously published forecasts for 1981–86 was very similar to that of the means and weighted means of the individual methods (Table 1, Fig. 3).

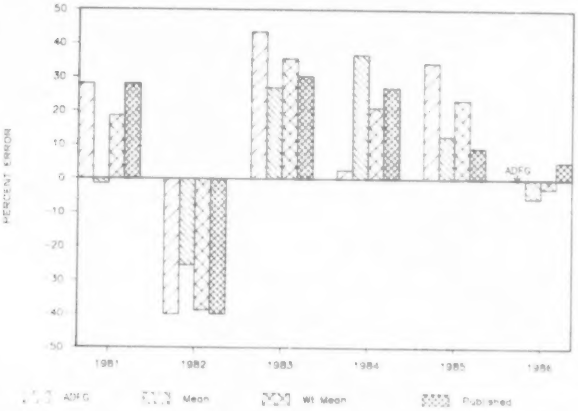

FIG. 3. Percent errors of four ways used to forecast numbers of sockeye salmon returning to Bristol Bay, Alaska, 1981–86. ADFG = Previously published Standard Alaska Department of Fish and Game forecasts based on spawner-recruit, sibling, and smolt data; Mean = Mean of ADFG and JRVC-0 (hindcasts of two- and three-ocean returns based on Japanese research vessel catches of immature sockeye salmon) estimates; Wt Mean = Weighted mean of ADFG and JRVC-0 estimates; Published = Previously published forecasts used by ADFG to set preseason management plans (Standard ADFG method results used for 1981 and 1982; weighted mean of Standard ADFG results and those of other methods used for 1983–86).

KVICHAK RIVER

The smolt model performed slightly better than either the spawner-recruit or sibling models in forecasting total sockeye salmon returns to the Kvichak River system during 1980–86 (Table 2 and Fig. 4). The smolt model had a much lower SE value than either of the other two models and lower ab-

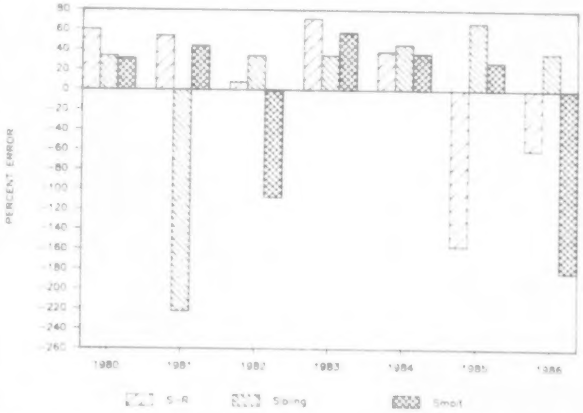

FIG. 4. Percent errors of three linear regression models used to forecast numbers of sockeye salmon returning to the Kvichak River, Bristol Bay, Alaska, 1980–86. S-R = Hindcasts based on spawner recruit model; Sibling = Hindcasts based on sibling model; Smolt = Hindcasts based on smolt model.

TABLE 2. Performance of three methods of forecasting total sockeye salmon returns to the Kvichak River system, Bristol Bay, Alaska, 1980–86. Spawner-recruit, (S-R), sibling, and smolt method results were based on hindcasted estimates. (MPE = mean percent error, MAPE = mean absolute percent error, SE = standard error of regression), the most accurate forecast method value is underlined. Forecast methods and performance measures are explained in the text.

Performance measure	Forecast method			Mean	Weighted mean[a]	Published forecast
	S-R (1)	Sibling (2)	Smolt (3)	1+2+3	1+2+3	
MPE	1.7	4.2	−14.1	−14.8	−14.2	−56.3
MAPE	64.4	67.7	70.3	53.7	52.9	90.8
SE	12.2	8.3	3.1	3.7	4.0	7.2

[a] Weighting factor used each year was regression variance for forecasted (independent variable) versus actual returns (dependent variable), for all years prior to, but not including, the year of interest.

solute percent errors for 4 of the 6 yr examined. All three models tended to under-forecast returns (sibling in 6 out of 7 yr; spawner-recruit and smolt in 5 out of 7 yr), although the two large overforecasting errors made by the smolt model (in 1982 and 1986) resulted in a negative MPE value. The spawner-recruit model had the lowest MPE and MAPE values, but only had the lowest absolute percent error 1 (1982) out of 7 yr.

Pooling results of all three models (either by calculating means or weighted means) resulted in forecasts with MAPE values lower than any of the individual models and with MPE and SE values only slightly greater than the smolt model (Table 2). There was no clearly defined superiority in performance between the mean or weighted mean of forecast methods. MPE, MAPE, and SE values, as well as yearly absolute percent errors (Fig. 5), were very similar for mean and weighted mean forecasts. Also, both mean and weighted mean forecasts had equal numbers of underforecasting (3 out of 7 yr) and overforecasting (4 out of 7 yr) errors.

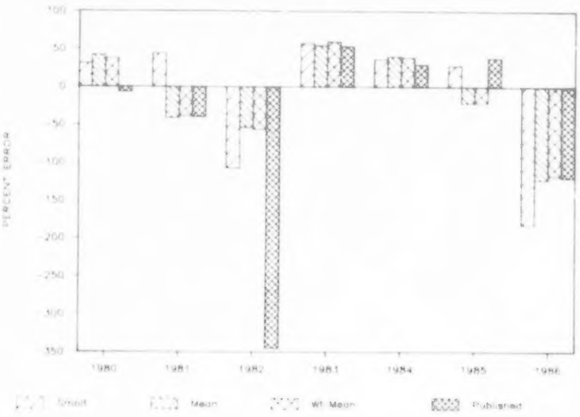

FIG 5. Percent errors of four ways used to forecast numbers of sockeye salmon returning to the Kvichak River, Bristol Bay, Alaska, 1980–86. Smolt = Hindcasts based on smolt linear regression model; Mean = Mean of results from spawner-recruit, sibling, and smolt linear regression models; Wt Mean = Weighted mean of results from spawner-recruit, sibling, and smolt linear regression models; Published = previously published Standard ADFG forecasts based on mean of results from spawner-recruit, sibling, and smolt models (including results from several models no longer used).

Performance of previously published forecasts for 1980–86 was much worse than that of either mean or weighted mean forecasts (Table 1, Fig. 5). This was due to an extremely large overforecasting error for the published ADFG forecast in 1982.

Discussion

We know of only one other investigation, a study done by Brannian et al. (1982) on Egegik River sockeye salmon, which examined pooling as a method to increase the accuracy of preseason Pacific salmon forecasts. This was surprising, since pooling is commonly used as a forecasting tool in economics and business management (Armstrong 1978). Results of our study have shown that forecasts of sockeye salmon returns based on means or weighted means of estimates from different methods were more accurate than forecasts based on any of the individual estimates. Increased accuracy of pooled forecasts was in many cases due to the absence of very large errors as well as improved year-to-year accuracy.

We were particularly encouraged by the increase in accuracy observed for Kvichak River system forecasts when using either the mean or weighted mean to pool results of spawner-recruit, sibling, and smolt models. These pooled forecasts were also more accurate than previously published ADFG forecasts, which indicated that the use of a single regression model for each data source produced more accurate forecasts than did the past practice of using two or more different models for each data source. For example, the 1984 Kvichak River system forecast based on smolt data was calculated as the mean of results from three different mean of ratios estimators (Eggers et al. 1983b).

Mathews' (1961) economic evaluation of Bristol Bay sockeye salmon forecasts suggested that improvements in accuracy of individual system forecasts, rather than a total Bristol Bay forecast, would provide the greatest future economic gains to the fishing industry. Unfortunately, changes which have occurred within the fishing industry since the time of Mathews' (1961) study (e.g. shifts from product canning to freezing, from land-based to vessel-based processing, from company to independent fishermen, etc.), have made his monetary estimates of benefits less useful for evaluating our results. While we did not attempt to provide an updated estimate of costs and benefits to be obtained from improvements in forecast accuracy, application of the analysis procedures presented in our study should result in total Bristol Bay and individual river system forecasts which, on average, should be within about 20 and 50%, respectively of actual sockeye salmon returns. This represents a substantial gain in forecast accuracy through the use of data which are already routinely collected, without the addition of new field projects. We think it is unlikely that further large gains in forecast accuracy will be made using other analytic techniques, such as time series analysis, on available data. Further advances in forecasting accuracy may only be possible through detailed studies concerning the production and survival of sockeye salmon in both the marine and freshwater environments. Unfortunately, such studies will be expensive, difficult to conduct, and must span a period of several years to provide sufficient data for analyses.

Aknowledgements

We thank the staff associated with the Alaska Department of Fish and Game, United States Fish and Wildlife Service, National Marine Fisheries Service, University of Washington, and Fisheries Agency of Japan who over the years have helped to collect and compile the data which have made the Bristol Bay sockeye salmon forecasting program possible.

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The Utility of Babine Smolt Enumerations In Management of Babine and Other Skeena River Sockeye Salmon (*Oncorhynchus nerka*) Stocks

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Abstract

MACDONALD, P. D. M., H. D., SMITH. AND L. JANTZ. 1987 The utility of Babine smolt enumerations in management of Babine and other Skeena River sockeye salmon (*Oncorhynchus nerka*) stocks, p. 280–295. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Pre-season forecasts of the numbers of adult sockeye salmon (*Oncorhynchus nerka*) returning to the Skeena River have utilized estimates of the numbers of seaward-migrating juveniles (smolts) leaving Babine Lake, the primary nursery area. These forecasts have often been unsatisfactory. Using data on production, catch, and escapement for brood years 1943–84 (including smolt data for brood years 1959–83), we study the forecasting problem in two different ways: forecasting the accumulated return (over several calendar years) of fish from a given brood year, and forecasting the total return (which includes components from several brood years) in a given calendar year. Peterman's (1982a) observation of highly variable smolt-to-adult survival is confirmed, but the pattern of odd/even year differences he found appears to have been disrupted in recent years. The relationships which predict future returns from a given brood year are much less well-defined that those which predict total return in a given calendar year. Stepwise regression analysis shows that the best pre-season forecast of total return in given calendar year is one based on the number of jacks (3-yr-old males) returning in the previous year and the number of smolts migrating to the ocean 3 yr previously. Since the onset of the Babine Lake Development Project, the average return has increased by about a million fish per year, but the variablility in the return has also increased to the point where returns have become almost impossible to predict from these data series alone. This variability may be related to a decrease in the average size of the migrating smolts. There is not much that could be done to improve the smolt enumeration field operation that would be cost-effective: variable marine survival is the major source of uncertainty in the forecasts.

Résumé

MACDONALD, P. D. M., H. D. SMITH. AND L. JANTZ. 1987. The utility of Babine smolt enumerations in management of Babine and other Skeena River sockeye salmon (*Oncorhynchus nerka*) stocks, p. 280–295. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les prévisions de pré-saison du nombre de saumons nerkas adultes (*Oncorhynchus nerka*) revenant dans la rivière Skeena ont été basées sur des estimations du nombre de saumons juvéniles (smolts) se dirigeant vers la mer à partir du lac Babine, la plus importante zone de croissance. Ces prévisions se sont souvent avérées insatisfaisantes. Les auteurs ont utilisé des données relatives à la production, aux prises et aux échappées pour les années de ponte de 1943 à 1984 (y compris des données sur les smolts pour les années de ponte 1959 à 1983) afin d'étudier les problèmes de prévision de deux façon différentes : la prévision du nombre total de poissons d'une année de ponte donnée revenant dans la rivière (au cours de plusieurs années) et la prévision du nombre total de poissons (de plusieurs années de ponte) y revenant au cours d'une année donnée. On a ainsi confirmé l'observation faite par Peterman (1982a), à savoir la grande variabilité du rapport de survie smolts à adultes, mais il semble que l'allure des écarts annuels entre les années impaires et paires qu'il avait notée se soit modifiée au cours des dernières années. Les relations qui permettent de prévoir les retours des poissons d'une année de ponte donnée sont beaucoup moins bien définies que celles permettant de prévoir les retours totaux au cours d'une année donnée. L'analyse par régression séquentielle a permis de montrer que la meilleure prévision de pré-saison du nombre total de poissons revenant dans la rivière au cours d'une année donnée était celle qui était basée sur le nombre de mâles âgés de trois ans étant revenus au cours de l'année précédente et sur le nombre de smolts ayant migré vers l'océan trois ans auparavant. Depuis la mise en marche du projet de mise en valeur du lac Babine, le nombre moyen de poissons étant revenu s'est accru d'environ 1 million par an, mais la variabilité des remontées a aussi augmenté à un point tel qu'il est pratiquement devenu impossible de les prévoir à partir de cette seule série de données. Cette variabilité peut être liée à une baisse de la taille moyenne des smolts en migration. Il est pratiquement impossible d'améliorer de façon rentable le dénombrement des smolts sur le terrain, la survie en mer, qui est variable, constituant la principale source d'incertitudes des prévisions.

Introduction

Sockeye (*Oncorhynchus nerka*) smolt runs from Babine Lake, British Columbia, have been enumerated annually since 1961 using a consistent mark–recapture technique (Jordan and Smith 1968; Macdonald and Smith 1980). This sampling program has also permitted close monitoring of the size and condition of migrating smolts. In conjunction with the excellent catch and escapement data series that are available for Babine and other Skeena stocks, the Babine smolt data provide a unique opportunity to assess the utility of smolt data for two important management purposes: pre-season forecasts of adult returns and monitoring freshwater growth and survival.

There has been a directed commercial fishery for Skeena sockeye since 1877. The catch and escapement data go back to the 1940's and the catch data alone go back to 1904. Age composition, size, and other characteristics of the runs have been assessed since about 1912 and a test fishery has provided indices of escapement since 1955. In the areas where Skeena stocks are harvested, the degree of mixing with other stocks is relatively low, hence the data on Skeena returns will be among the more reliable data sets when all major Pacific coast sockeye runs are considered. The only reservation is that, in recent years, substantial numbers of Skeena sockeye have been caught in the southeastern Alaska fishery, and totally reliable catch and age-composition data are not yet available for these interceptions. The dynamics of Skeena adult stocks have been described by Godfrey (1958), Shepard and Withler (1958), Larkin and McDonald (1968), Ricker and Smith (1975), and Peterman (1982a). Johnson (1965), McDonald (1969), McDonald and Hume (1984), and Macdonald and Smith (1980) have studied the juveniles of Babine Lake. Levy and Hall (1985) review 40 years of limnology and sockeye ecology investigations at Babine Lake.

Artifical spawning channels established on the Fulton River and Pinkut Creek systems (Fig. 1) in the early 1970's comprise the Babine Lake Development Project (West 1978) and these have greatly increased the production of Babine Lake fry and smolts. The catch and escapement data series provide a means of measuring the impact of the project and evaluating its effectiveness in terms of enhanced returns. The smolt data will reflect any consequential changes in freshwater growth and survival.

Babine smolt numbers would appear, at first sight, to be useful for pre-season forecasting of Skeena sockeye runs. In recent times, the Babine stock has accounted for 95% or more of all Skeena production. More than 95% of these fish have emigrated after a single year of lake residence and virtually all return after either one, two, or three winters at sea, so a rather limited number of fresh- and saltwater age-groups need to be taken into account (McDonald and Hume 1984). The physical configuration of the lake outlet and the behaviour of smolts there are conducive to accurate enumeration (Macdonald and Smith 1980). Finally, having a forecast tool several years in advance of returning runs is very appealing for planning purposes and has met with some success elsewhere. For instance, Fried and Yuen (1987) found numbers of smolts to be among the best forecast tools for the large Kvichak River run in Bristol Bay. Counts of spawners, eggs, or fry share many of the same potential advantages as counts of smolts, but will tend to be less useful because of variable mortality during the intervening stages.

Despite these appealing factors, Babine smolt numbers have not yet proved to be very useful indices for the Babine and Skeena runs. Peterman (1982a) analysed brood years 1960–76, found considerable variability in smolt-to-adult survival, and discussed the possibility that there is significant density-dependent mortality, probably in the first 15 mo of marine life. McDonald and Hume (1984) confirmed this with an additional brood year (1977). They expanded on Peterman's observation that returns from odd-numbered brood years were much better correlated with smolt numbers than were those from even-numbered brood years, though the reasons for this phenomenon remained purely speculative.

For this paper, we have assembled data for brood years 1943–84, including smolt data for brood years 1959–83 (that is, the smolt runs in years 1961–85). We study the forecasting problem in two different ways: forecasting the accumulated return (over several calendar years) of fish from a given brood year, and forecasting the total return (which includes components from several brood years) in a given calendar year. The first way, which concerns the accumulated successes of a given brood, is the more relevant when discussing the effect of the Babine Development program, for example. The second is the more relevant for setting quotas for the fishery in a given year, and for related management planning purposes.

Methods

The North American system of age designation is used here. It expresses total age as a numeral, with a subscript to indicate the number of years spent in freshwater. All age designations given in this paper apply to "sub 2" fish (1. by the European system) unless stated otherwise.

BABINE SMOLT ENUMERATIONS

Sampling is done from a platform at the north end of Nilkitkwa Lake, where it flows into the Babine River. The map of Babine Lake shown in Fig. 1 indicates how, in a typical year, the smolt run is divided into an "early" run from the North Arm and Nilkitkwa Lake, and a "late" run

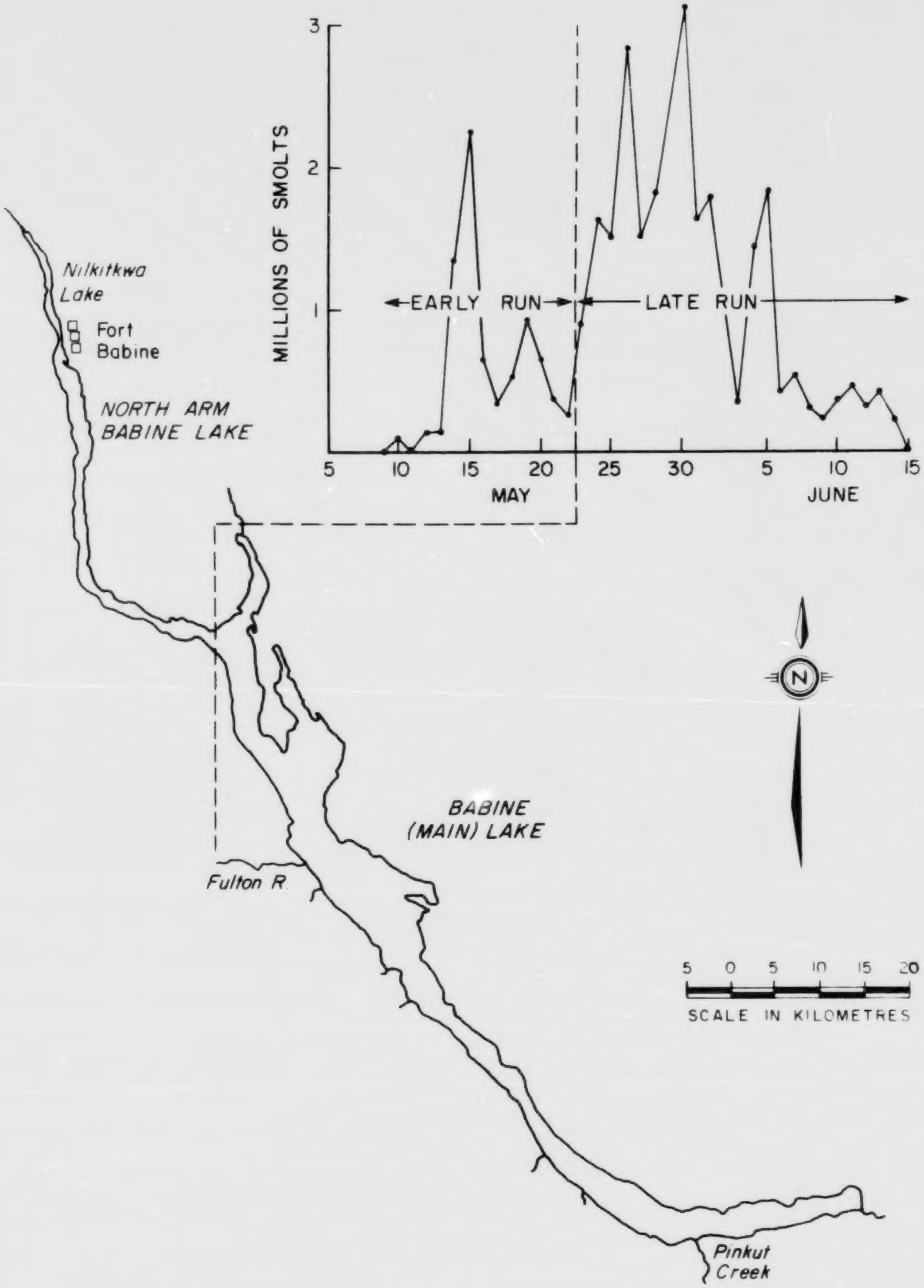
3
2
1
MILLIONS OF SMOLTS
EARLY RUN
LATE RUN
5
10
15
20
25
30
5
10
15
MAY
JUNE
Nilkitkwa Lake
Fort Babine
NORTH ARM BABINE LAKE
BABINE (MAIN) LAKE
Fulton R.
Pinkut Creek
N
5 0 5 10 15 20
SCALE IN KILOMETRES

FIG. 1. Babine and Nilkitkwa lakes, showing areas of origin and typical timing of the early and late smolt runs, and the locations of the Babine Development Project streams, Fulton River and Pinkut Creek.

from the main lake. The division point between the two runs is often poorly defined, but can usually be determined with some confidence to within a day or two. It is characterized by a lull in activity and a change in smolt behaviour, the late-run or main lake smolts being slightly larger, less easily alarmed, and exhibiting more persistent migration intensity. In years where there is no lull in activity between the early and late runs, the onset of the late run is marked by a rather steady increase in the average length and weight of migrants, which suggests that there is some overlap rather than a clear division.

The Research Branch and the operational branch of the Department of Fisheries and Oceans have each, at various times, been responsible for the Babine smolt enumeration program, but the field methodology has been consistent from 1961 to the present time. A portion of each daily run is captured at the lake outlet, tagged with staple tags (Jordan and Smith 1968) so that the tagged fish are identifiable by day of release, and re-introduced into the population 3-4 km upstream in Nilkitkwa Lake. This creates a flow of marked fish mixed with the migrating unmarked fish, and daily sampling at the lake outlet provides marked/unmarked ratios from which daily run estimates can be computed. The analysis is complicated by the fact that the number of marked fish migrating past the sampling platform on a given day, either from a given day of release or in total, is not directly measureable and cannot be estimated without making assumptions about how marked smolts behave after they are released upstream.

Daily estimates are summed to give totals for each of the early and late runs, and for the year. On most days, 100–150 fish are also sampled for such determinations as length, weight, and prevalence of certain parasites. Daily averages are weighted by daily abundance to give average length and weight for the early and late components of the run and for the total run.

Run estimates provided to other authors (e.g. Peterman 1982a; McDonald and Hume 1984) were computed using H.D. Smith's original analysis, called the "constant sampling fraction" model by Macdonald and Smith (1980). We now prefer the "parsimonious" model analysis of Macdonald and Smith (1980), which fits a probability distribution for the number of days a marked smolt spends back in the lake before making its second attempt to migrate. For this paper, we have extended that analysis by fitting separate probability distributions to each of the early and late runs, to reflect differences in smolt behaviour. The division point was estimated as the date that gave the best fit of the overall model (including both early and late runs) to the data. The estimated date was generally within a day or two of the division point previously established by field staff on the basis of other criteria (numbers, size, and behaviour). The old and new estimates are compared in Table 1. For total run, the agreement has been very close for the past 6 years, presumably the result of greater standardization of field enumeration procedures. For the majority of years the percentage difference between the old and new estimates is not unduly large relative to the coefficient of variation for the new estimate. Generally speaking, an unusually large coefficient of variation can be attributed to unusually low numbers of recaptures in that year, while an unusually high percentage difference between the old and new estimates indicates that assumptions of one

TABLE 1. Babine smolt estimates generated by two models. (a) as developed in 1970 and used until now in Skeena sockeye stock management, and (b) the "parsimonious model" of Macdonald and Smith (1980), extended to allow for differences in the early and late runs, now the preferred analysis. Runs are in millions of smolts. C.O.V. denotes coefficient of variation.

Brood year	Early run		Late run		Total runs			
	(a)	(b)	(a)	(b)	(a)	(b)	% diff	C.O.V. of (b)
1959	6.12	8.26	13.13	13.17	19.25	21.43	11.3	8.1
1960	1.73	3.92	13.68	17.00	15.41	20.92	35.8	22.2
1961	8.68	6.73	5.78	6.43	14.46	13.16	−9.0	5.3
1962	16.54	20.22	29.35	41.51	45.89	61.73	34.5	15.6
1963	5.72	3.38	19.16	28.20	24.88	31.58	26.9	6.3
1964	21.52	20.09	13.78	13.10	35.30	33.19	−6.0	4.4
1965	9.72	10.65	6.84	7.47	16.56	18.12	9.4	4.2
1966	13.79	15.58	18.10	19.45	30.89	32.03	3.7	8.6
1967	22.00	23.98	24.18	28.18	46.18	52.16	12.9	7.3
1968	8.37	13.87	34.63	38.54	43.00	52.41	21.9	6.6
1969	13.30	17.95	39.20	38.73	52.50	56.68	8.0	2.5
1970	9.11	13.83	44.56	37.42	53.67	51.25	−4.5	4.0
1971	16.05	16.64	73.98	88.97	89.03	105.62	18.6	4.1
1972	18.97	26.23	61.13	78.51	80.10	104.74	30.8	2.6
1973	5.67	4.90	27.43	33.23	34.10	38.12	11.8	2.9
1974	6.87	7.06	36.12	38.42	42.99	45.48	5.8	8.4
1975	10.03	10.25	51.02	54.66	61.04	64.90	6.3	3.8
1976	5.05	10.06	70.59	80.89	75.63	90.95	20.3	7.8
1977	9.04	11.00	99.19	112.44	108.23	123.44	14.1	3.3
1978	7.56	2.33	47.64	55.35	55.20	57.68	4.5	4.4
1979	12.10	12.96	185.80	178.76	197.90	191.72	−3.1	9.5
1980	13.78	14.86	117.08	122.26	130.86	137.12	4.8	8.6
1981	11.20	3.59	140.10	142.63	151.30	146.22	−3.4	14.6
1982	15.59	19.73	81.23	79.29	97.16	99.02	1.9	23.2
1983	6.35	7.39	45.08	42.44	51.43	49.83	−3.1	5.5

or both of the two analyses were violated. The most likely violation is that a constant fraction of the run was not sampled each day, hence our preference for the new estimates as they do not depend on this assumption.

Agreement between the old and new estimates of the early run size is sometimes quite poor. This is because there were years in which there was no lull between the early and late runs, and changing the assumed division point even by one day can make a very large percentage difference in the estimate of the early run. If the late run is much larger than the early run, the late-run estimate will be less affected. Hence, choosing the best division point deserves further study, albeit retrospectively for historical data.

Both the old and new estimates assume that mortality of tagged fish is negligible, at least for the first few days after release, and this has been confirmed a number of times by holding fish in pens for a few days after marking (Jordan and Smith 1968; H.D. Smith personal communication). If there were years in which field procedures led to a significant tagging mortality, the runs in those years were probably overestimated (Macdonald and Smith 1980).

DATA ON FRY PRODUCTION

Fry counts from Fulton River, Pinkut Creek, and their associated spawning channels, 1970–85, were provided by C.J. West, Department of Fisheries and Oceans, Vancouver, B.C. V6E 2P1. Fry counts from other Babine spawning areas are not available, but, at least for these years, the Fulton River and Pinkut Creek fry account for most of the production in the main basin of Babine Lake, and their numbers will be shown to be highly correlated with the smolt run one year later.

An estimate of all Main Lake fry production is possible by determining the spawning potential outside the Development Project and assuming a mean of 233 fry per spawner in the manner of McDonald and Hume (1984, p. 72). The non-Development Project spawning escapement is considered to be the difference between the total late run escapement at the Babine counting fence and the numbers accounted for in the project streams. This includes variable numbers of lake spawners with a level of production which is uncertain, but potentially very high in some recent years. (See West and Mason 1987, for further discussion.)

NUMBERS AND AGE COMPOSITION OF RETURNING ADULTS: CATCH AND ESCAPEMENT

Escapement data come from the test fishery (since 1955) and from complete enumeration of returning Skeena River adults at the Babine counting fence. The fence was first constructed in 1945 and crosses the Babine River 1 km below the outlet of Nilkitkwa Lake. Samples are often taken at the fence and from various spawning grounds (e.g. from the Development Project) and, along with test fishery samples, these can be used to determine the age composition of the escapement very accurately.

Samples of the catch are taken in an annual port sampling program, but they pose more of a problem. The major exploitation occurs in the intense commercial seine and gillnet fishery at the approaches to the Skeena River and in the estuary. In the period 1980–85, this catch averaged over one million sockeye per year. Other Skeena sockeye are taken incidently in troll fisheries (about 25 000 – 50 000 per year), in the southeastern Alaska seine and gillnet fishery at Noyes Island and Cape Fox (about 225 000 per year), and in the Nass River gillnet fishery (about 200 000 per year). Indian food fishery gillnets take another 100 000 – 200 000 annually. The high seas fishery is negligible (Fredin 1980), as is the sports fishery.

In the mixed fisheries, the Skeena stocks must be distinguished from other sockeye, but partitioning cannot be done with certainty. Some fisheries, such as the Indian food fishery, are not sampled for age composition, and in all fisheries there are problems in determining numbers and age composition on the basis of limited and possibly non-representative samples. The southeastern Alaska data had to be omitted from certain of our analyses for these reasons, even though this fishery may have accounted for as much as 15% of all Skeena stock returns since 1980.

Most of the data we have used are on file with the Department of Fisheries and Oceans in Prince Rupert. Table 2 shows the total of catch and escapement (catch summed over all fisheries), broken down by age at return. Performance of the Skeena River stock relative to fry and smolt production from the Babine Main Lake region is summarized in Fig. 2. A more detailed breakdown may be obtained from one of the authors (L. Jantz).[1]

The commerical catch in Fisheries Management Area 4 (Skeena estuary and approaches) for the period 1940–83 was taken from Department of Fisheries and Oceans statistics (Circular Series No. 25 for 1940–50). Age composition was determined from scale samples taken in the port sampling program.

The commercial catch in the outer portions of Area 3X and 3Y, adjacent to the Nass River, was determined in the same manner, but with the added complication of distiguishing Skeena from Nass River stocks. Tagging programs and racial analysis done in several years have indicated a division point around July 15, plus or minus a few days, and all catches in the fishing periods after July 15 are usually attributed to the Skeena River.

The native Indian food fishery occurs along the Skeena River and in some of its tributaries and lakes, including Babine Lake. Most of the catch is by commerical-sized gill nets, so the age composition of the commercial fishery is assumed to apply. We have taken numbers for 1940–48 from Shepard and Withler (1958), and for 1949–85 from Management Biology files in Prince Rupert.

The jack sockeye (small males aged 3_2) are seldom caught in commercial or native Indian gillnet fisheries because of their small girth, but unrecorded numbers are also taken in the seine fishery and some are caught in panels of small mesh in the test fishery gillnets. We have taken the numbers tallied at the Babine counting fence to represent all Skeena jacks, despite the possibility of error if seine catches of this age-group are substantial, or highly variable from year to year. Catches in an Indian "jack fishery" at the counting fence are included in this count. The proportion of jacks in the Development Project escapements has increased in recent

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[1] Final 1986 adult returns became available after our calculations and text figures were prepared. We have added these returns to Table 2 (brood years 1981–83) but not to the figures, and they were not included when calculating correlation coefficients.

TABLE 2. Skeena sockeye returns from brood-year escapement. Alaskan catches are not included. The 1984 and 1985 data are preliminary.

Brood year	Brood escapement	Number in returns					
		3_2(jack)	4_2	5_2	Combined	3_2+4_2	4_2+5_2
1943	272 000	31 000	130 643	306 008	467 651	161 643	436 651
1944	824 000	261 000	2 070 964	1 001 243	3 333 207	2 331 964	3 072 207
1945	940 000	NO COUNT	258 546	698 000	956 546		956 546
1946	486 000	48 000	235 223	698 735	981 958	283 223	933 958
1947	307 000	179 000	472 845	498 041	1 149 886	651 845	970 886
1948	1 066 000	11 000	1 841 515	415 905	1 268 420	1 852 515	2 257 420
1949	480 000	28 000	932 094	513 883	1 474 976	960 094	1 445 976
1950	393 407	28 000	521 397	164 691	714 088	549 397	686 088
1951	219 395	10,000	51 626	74 668	136 294	61 626	126 294
1952	420 850	31 000	482 463	222 926	736 389	513 463	705 389
1953	706 920	18 000	562 466	888 569	1 469 035	580 466	1 451 035
1954	510 515	50 000	670 299	773 023	1 493 322	720 299	1 443 322
1955	87 077	31 000	238 660	140 173	409 833	269 660	378 833
1956	370 018	32 000	343 420	353 870	729 290	375 420	697 290
1957	448 144	49 000	1 567 627	629 563	2 245 890	1 616 327	2 196 890
1958	819 260	28 000	514 624	165 075	707 699	542 624	679 699
1959	799 332	46 000	608 488	1 182 980	1 837 468	654 488	1 791 468
1960	273 161	173 000	462 400	313 122	948 522	635 400	775 522
1961	935 535	60 000	649 237	485 637	1 194 874	709 237	1 134 874
1962	558 370	64 000	545 074	940 524	1 549 598	609 074	1 485 598
1963	597 467	182 000	974 963	1 270 847	2 427 810	1 156 963	2 245 810
1964	848 215	29 300	198 948	510 684	738 932	228 248	709 632
1965	619 180	53 400	746 289	402 410	1 202 099	799 689	1 148 699
1966	319 159	154 000	822 813	704 125	1 680 938	976 813	1 526 938
1967	599 060	166 000	1 040 673	1 067 000	2 273 673	1 206 673	2 107 673
1968	565 302	54 600	369 497	942 266	1 366 363	424 097	1 311 763
1969	654 582	258 700	1 149 524	1 505 001	2 913 225	1 408 224	2 654 525
1970	633 068	233 400	849 065	370 652	1 453 117	1 082 465	1 219 717
1971	775 876	254 369	1 104 248	810 036	2 168 653	1 358 617	1 914 284
1972	674 497	136 995	555 475	1 092 708	1 785 178	692 470	1 648 183
1973	782 824	225 458	958 216	739 311	1 952 985	1 213 674	1 697 527
1974	719 881	45 500	223 149	299 266	567 815	268 549	522 415
1975	819 766	296 300	2 326 695	842 992	3 465 987	2 622 995	3 169 687
1976	566 338	93 400	227 754	371 221	692 375	321 154	598 975
1977	926 374	233 885	2 815 098	2 613 545	5 662 528	3 048 983	5 428 643
1978	397 121	155 549	534 599	945 379	1 635 527	690 148	1 479 978
1979	1 126 228	60 217	585 329	755 380	1 400 926	642 546	1 337 709
1980	517 672	353 138	1 300 457	3 279 219	4 932 814	1 653 595	4 579 676
1981	1 391 176	120 088	1 453 207	956 346	2 529 641	1 373 295	2 409 553
1982	1 104 597	66 714	515 987			582 701	
1983	864 620	87 125					
1984	1 020 689						
1985	2 159 740						

years, perhaps as a result of their relatively low vulnerability to fishing, in a situation where the total stock is increasing and there is a corresponding increase in the catch of older fish.

STATISTICAL ANALYSES

All analyses were done with log-transformed data. Peterman (1982a, 1982b) recommends this because it is appropriate if the error structure is multiplicative with a lognormal error distribution and because density-dependent survival rates will show as departures from unit slope on a log-log plot of numbers at two different life stages. By way of a "sensitivity analysis", we have also repeated some of our analyses using untransformed and square-root transformed data, but our main conclusions remain unchanged.

The simplest possible predictor of total return in a given year is the historical average, or a fitted time series if there is autocorrelation (Box and Jenkins 1970). Because of changes brought on by the Development Project, only data from about 1973 onwards should be used for current projections of this type. This does not give a series long enough for effective forecasting so, as a compromise, data from 1964 to 1984 were used. Box-Jenkins time series analysis was done using MINITAB 82.1 software (MINITAB Inc., State College, Penn., USA).

Relations between different life stages, and between numbers at a given life stage and total returns, were studied with simple linear regression and correlation on log-transformed numbers. The usual statistics for these analyses include Pearson's correlation coefficient, r; the relative reduction in variance due to regression, r^2; the fitted slope,

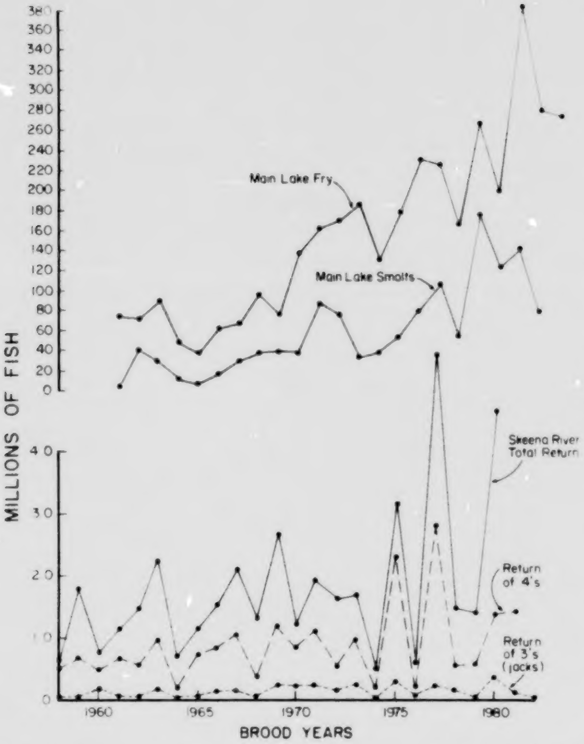

FIG. 2. Numbers of fry and smolts from the main lake basin of Babine Lake and returns by brood year of Skeena River sockeye of age 3_2, age 4_2, and ages 3_2, 4_2, and 5_2 combined.

b; and the *F*-test of the hypothesis that the true slope is zero. Correlation analysis is appropriate for measuring the degree of association in bivariate data, while regression analysis is appropriate when one variable is to be used as a linear predictor of the other: for example, when smolt numbers are to be used to predict later returns from a brood year, with the relationship assumed to be linear on a log–log plot. (When one variable is controlled and the other is a measured response, only regression analysis is appropriate, but this case does not arise here.) The two analyses are closely related. In particular, the effectiveness of the regression in reducing variance is measured by r^2, the square of the correlation coefficient, and the *F*-statistic for testing whether the slope *b* is significantly different from zero can be computed as $F_0 = (n - 2)\, r^2 / (1 - r^2)$, where *n* is the number of observations. The *F* test is on 1 over $n - 2$ degrees of freedom. It also tests whether the correlation is significantly different from zero.

Peterman (1978, 1981, 1982a, 1982b) discusses in some detail how to test the hypothesis that the true slope is unity, since this corresponds to the hypothesis that mortality between the two life stages is independent of population density. The usual statistic for testing the hypothesis of unit slope in simple linear regression can be written $F_1 = (b-1)/b^2\, F_0$, an *F* test on 1 over $n-2$ degrees of freedom, but this test is not satisfactory unless there is a strong correlation ($r > 0.9$, say). When the correlation is weaker than that, the points form a cloud of ill-defined orientation on the graph: while *b* is still the slope of the best linear predictor, it is not a good estimate of the slope of the underlying functional relationship.

For most analyses, it is only necessary to quote *n* and *r*. The reader may then compute r^2, F_0, and even a significance level for the *F* test, if desired. We have given significance levels for cases where the reader may be tempted to compute them, but, on the whole, we do not believe that significance tests should be relied upon too heavily in work of this nature, for two reasons. The first is that the assumptions of independence, constant variance and normality (or log-normality of the untransformed data) cannot really be assumed to hold for these data. The second is that a significance test tends to be as much a measure of sample size as a real test of truth or falsehood of the hypothesis. In the natural sciences, models are at best approximate and no quantitative hypothesis will be true in an exact mathematical sense. Hence, unless the hypothesis is blatantly false (in which case no statistical test is required) the hypothesis has a high probability of being accepted when the sample size is small but is certain to be rejected when the sample size is sufficiently large.

This is not to say that statistical rigour is unnecessary. On the contrary, the important problem of distinguishing between real effects and random noise remains. What we are saying is that to base a conclusion solely on whether the computed level of significance is above or below 5%, is to oversimplify the problem, especially when the assumptions underlying the test may not hold exactly and the accuracy of the computed significance level is not known. In a general way, we know that the relations studied in this paper are real. For example, if no smolts were to migrate to the ocean, then it would be certain that no adults would return, but if the data at hand do not extend to such extreme cases then measurement error and variable survival might well give the impression that no relationship exists, when in fact one does.

We prefer a more descriptive, graphical analysis, in the spirit of Green (1987). The most interesting of the relationships between the life stages are shown in figures presented below where each point is labelled with either the brood year or the year of return so that outliers and trends may be identified. To help give a visual impression of the strength of the relationship, the fitted least-squares line is shown, together with 95% confidence bounds for the true line (the inner bounds on the graph) and 95% prediction bounds for a single observation (the outer bounds) (Snedecor and Cochran 1967). The least-squares line is appropriate for predicting the value of the ordinate, given the value of the abscissa.

Stepwise multiple regression was performed using MINITAB 82.1, to select the predictor variables that give the most effective pre-season forecast of the total return in a given calendar year. Since the return will consist predominantly of the age-groups 4_2 and 5_2, the possible predictor variables will be the siblings and earlier life stages of these fish. These include the number of 4_2 fish returning 1 year prior (siblings of the current 5_2's), the numbers of jacks (3_2's) returning 1 year prior and 2 years prior, the numbers of smolts 2 years prior and 3 years prior, the numbers of fry 3 years prior and 4 years prior, and the spawning escapements 4 years prior and 5 years prior.

The pre-season predictor that results from stepwise regression can be evaluated by using all data up to the current year to predict the current year's return, but this will yield only one point of comparison. To simulate how the predictor would work had it been used from the beginning, by using, say, the first five years of data to predict the sixth year's return, then using the first six years to predict the seventh, and so on, is not a fair test because each comparison will be based on a different number of observations and the earliest ones may not even have enough observations to estimate the predictor. Thus we have repeatedly fitted the regression, first omitting the first year's data and using the regression to predict the return in the first year, then again, omitting the second year's data and using the regression to predict the return in the second year, and so on. This type of evaluation, based on the variability between subsets resampled from a single data series, is often referred to as a "jackknife" procedure (Efron 1982).

For each prediction, 95% limits were computed by the usual multiple regression formulae (Searle 1971). All of the predictions, their 95% prediction limits, and corresponding observed values, were then plotted on a graph.

Our information suggests that the mean size of late-run smolts has decreased more or less steadily since the onset of the Development Project. This is a case where a test of hypothesis is appropriate, since it is not obvious whether or not the decrease in size has gone on long enough to be considered a real trend rather than a chance event. An efficient nonparametric test was chosen for this purpose, Cox's (1955) S_1 test for trend.

Results and Discussion

FRESHWATER GROWTH AND SURVIVAL

The late smolt run now consists primarily of fish that originated in the Development Project spawning channels and spent one winter in the main basin of Babine Lake. Even before the spawning channels were constructed, 70% or more of the late run probably consisted of native fish of Pinkut Creek and Fulton River origin. There are also relatively small numbers of fish that originated in other, natural streams around the main basin. Also, some Development Project fish, and others, spawn in the lake, either because they do not reach the spawning channels or because they are turned away to avoid overcrowding, so in some years there may be considerable but unknown numbers of smolts from lake spawning. Despite this, it is generally valid to assume that the late smolt run represents Pinkut Creek and Fulton River fry production, and the numerical relationship between these life stages is shown in Fig. 3.

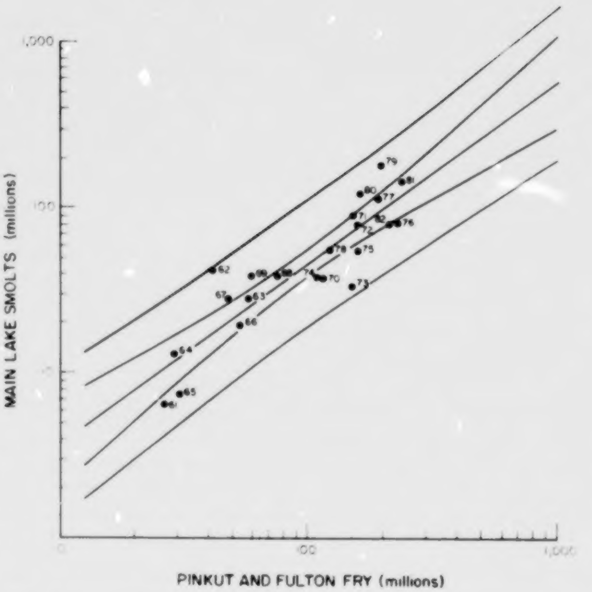

FIG. 3 Numbers of smolts from the main lake, Babine Lake, are plotted against fry production from the Development Project streams, on a log–log scale. Brood year (1961–82) is indicated for each point. The least-squares line is shown with 95% confidence bounds for the true regression line (the inner bounds) and 95% prediction bounds for a future observation (the outer bounds).

The relationship is very well defined ($r = 0.891$, $n = 22$, $F_0 = 76.9$, $P < 0.001$). The fitted slope is $b = 1.0906$, not significantly different from unity ($F_1 = 0.53$, $P = 0.48$). Thus there is no evidence of

TABLE 3. Estimated fry and smolt production, and fry–smolt survival, main lake, Babine Lake. Fry production outside the Development Project was estimated on the basis of 233 fry per spawner counted in main lake streams plus those from sockeye thought likely to have spawned in the lake proper. Fry and smolt estimates are in millions.

Brood year	Development Project fry	Total main lake fry	Main lake (late) smolts	Fry–smolt survival (percent)
1970	114.9	134.7	37.4	27.8
1971	152.1	161.2	89.0	55.2
1972	158.5	170.6	78.5	46.0
1973	150.7	183.2	33.2	18.1
1974	109.1	134.9	38.4	28.5
1975	158.3	174.6	54.7	31.3
1976	228.7	232.5	80.9	34.8
1977	190.6	230.9	112.4	48.7
1978	123.3	165.2	55.4	33.5
1979	197.0	262.7	178.8	68.1
1980	161.7	200.4	122.3	61.0
1981	237.5	380.8	142.6	37.4
1982	212.0	284.0	79.3	27.9
1983	117.9	276.9	42.4	15.3

density-dependent mortality between the fry and smolt stages. This implies that fry densities from brood years 1961–82 have not yet exceeded the carrying capacity of the main lake.

It is interesting to note that the pre-enhancement and post-enhancement years form distinct clusters on the graph. If the two groups of points were to be analyzed separately, the slopes would still be close to unity but the correlations would be much weaker than the correlation obtained for the combined data.

Points lying above the regression line in Fig. 3 represent higher-than-average fry-to-smolt mortality; points below the line represent lower-than-average mortality. In Table 3 we have extended McDonald and Hume's (1984, Table 1) data for Main Lake fry and smolt production for 7 brood years (1977–83). However our fry numbers include estimated numbers of lake spawners, thought to be particularly numerous in brood year 1981, while McDonald and Hume (1984) did not include this adjustment. Survival rates in some years are remarkably high; brood years 1979 and 1980, for example, have rates about twice as high as usual. This could be an artifact for any or all of four different reasons: the number of potential lake spawners may have been underestimated, the actual number of fry per potential lake spawner may have been higher than the assumed value of 233, the smolt run may have been overestimated as a result of high tagging mortality, or the date of the division point between the early and late smolt runs may have been set too early.

We feel it is unlikely that any of these explanations could account for the anomalous values. In particular, tagging mortality would have to remain high throughout an entire field season to affect the total estimate for that year appreciably, and we consider that unlikely in the extreme. Hence we are confident that the survival rates in Table 3 are valid.

The length and weight of early-run and late-run smolts has changed gradually since the 1959 brood year (i.e. the 1961 smolt run) (Fig. 4). The most striking feature is the apparent decline in both mean length and mean weight of the late-run smolts since 1971 when all spawning channels were fully operational. This was tested using Cox's (1955) S_1 statistic for trend, using the 12 points from the 1972–83 brood years, and there was evidence of a real decline if computed from either the length data or the weight data ($S_1 = 36$, $n = 12$, $z = 2.13$, one-sided $P = 0.02$). This is consistent with predictions of Johnson (1965) that mean size would decrease with increasing numbers of underyearlings. It also highlights the concern that smaller smolts might suffer a lowered marine survival rate, even though the lacustrine survival rate remains high.

There is some evidence of higher mortality among the smaller smolts, at least within a given brood. In 1967 and 1968, a total of 146 500 sockeye smolts, representing the full range of sizes in the runs, were tagged with magnetic coded-wire tags (C.W.T.) so that size group and day of tagging could be determined when they were recovered as adults. In all, 1 484 (1%) were recovered from the commercial fisheries and on the spawning grounds.

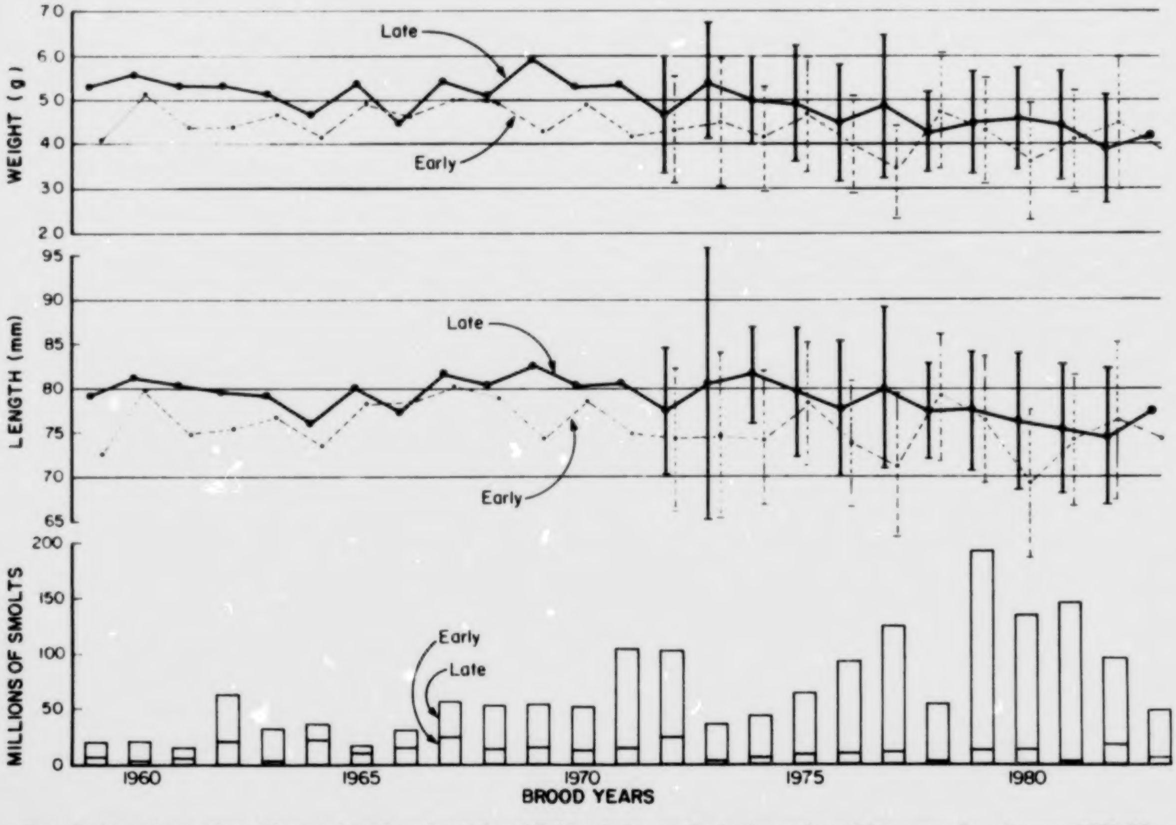

FIG. 4. Annual run size and mean length and weight of Babine Lake smolts in the early and late runs, brood years 1959–83.

TABLE 4. Recovery rates for tagged smolts in different size groups. Recoveries were of adults in the commercial fishery and on the spawning grounds.

Size group (mm)	1967			1968			Both		
	Tagged	Recovered	(%)	Tagged	Recovered	(%)	Tagged	Recovered	(%)
<75	9 000	45	(0.50)	16 100	29	(0.18)	25 100	74	(0.29)
>75-81	20 300	165	(0.81)	19 500	87	(0.45)	39 800	252	(0.63)
>81-87	23 000	348	(1.51)	20 100	200	(1.00)	43 100	548	(1.27)
>87	18 800	369	(1.96)	19 000	241	(1.22)	38 500	610	(1.58)
All	71 100	927	(1.30)	75 000	557	(0.74)	146 500	1 484	(1.01)

The results (Table 4) are similar for the two years and indicate that smolts smaller than about 80 mm in length were seriously disadvantaged. While there is evidence from unpublished smolt holding experiments conducted by one of us (H.D. Smith) at Babine Lake that tagging and handling mortality is slightly higher among fish in the smallest of these size categories, and one must also be cautious about extrapolating from within-year to among-year size groupings, it is not unlikely that the nearly 8 mm reduction in mean size of late run smolts over the 1969-83 brood years could have significantly affected their marine survival. Eventually, there should be clear targets for fry production which will maximize returns by balancing gains in smolt numbers against their declining size and reduced marine survival.

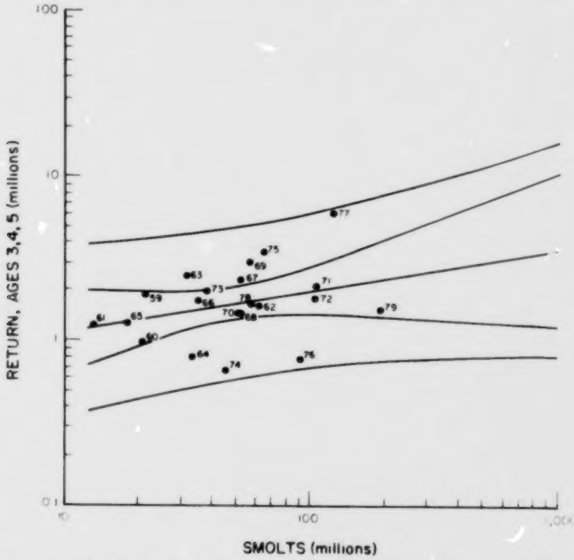

FIG. 5. Total return from each brood year, 1959-79, plotted against numbers of smolts. Same format as Fig. 3.

RELATIONS BETWEEN SMOLT NUMBERS AND RETURNS FROM A GIVEN BROOD YEAR

Total return from each brood year is plotted against the smolt run for that brood year in Fig. 5, extending similar graphs shown by Peterman (1982a) and McDonald and Hume (1984). The correlation is quite weak ($r = 0.326$, $n = 21$, $F_0 = 2.26$, $P = 0.15$).

The pattern of "odd year above the line, even year below the line" is evident with the exception of the 1966 and 1979 brood years. The strong relationship between smolts and returns from odd-numbered brood years, noted by McDonald

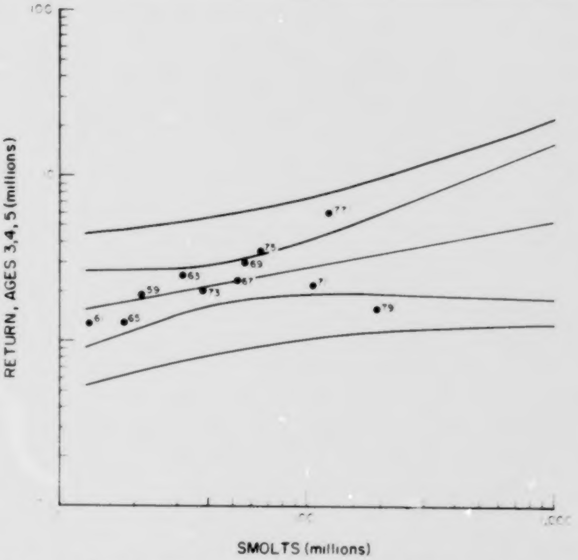

FIG. 6. Total return from each odd-numbered brood year, 1959-79, plotted against numbers of smolts. Same format as Fig. 3.

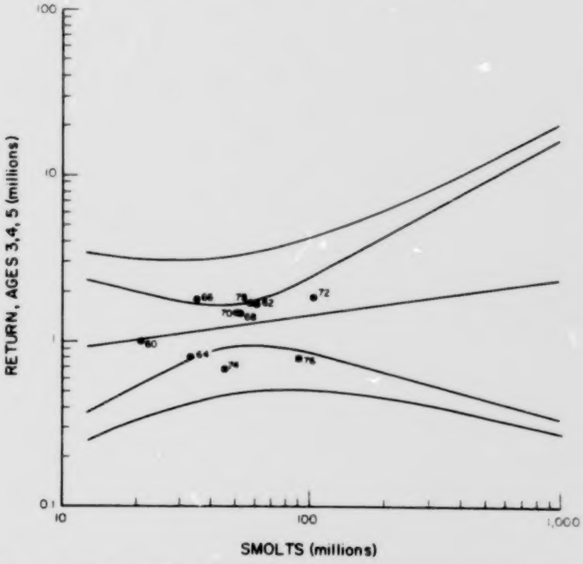

FIG. 7. Total return from each even-numbered brood year, 1960-78, plotted against numbers of smolts. Same format as Fig. 3.

and Hume (1984), is now weakened by the inclusion of 1979 ($r = 0.523$, $n = 11$, $F_0 = 3.39$, $P = 0.1$) (Fig. 6). There is certainly no evidence of any such relation for even-numbered brood years ($r = 0.262$, $n = 10$, $F_0 = 0.59$, $P = 0.46$) (Fig. 7). It is also interesting to note that the strong dominance in odd-numbered brood years noted by McDonald and Hume (1984) and others, was disrupted in returns of brood years 1979–81 (Fig. 2, Table 2) suggesting that this feature may be in the process of breaking down.

The scatter about the regression lines in Fig. 5–7 is the result of errors in measurement and estimation, as well as high variability in marine survival. The statistical error in the smolt run estimates is relatively small (Table 1) and there is reason to believe that factors such as tagging mortality, which might bias the estimates, are not a serious problem. There are more uncertainties in the estimates of total returns which take place over three calendar years and include fish from age-groups 3_2, 4_2, and 5_2. An accurate accounting of each age-group depends upon the accuracy with which the age composition of returns is determined in each of the those calendar years. As we have described above, not all components of the return are sampled thoroughly and there is the possibility that age composition is sometimes based on unrepresentative samples.

The percentages of fish returning at ages 3_2, 4_2, and 5_2 varies considerably from one brood year to another (Table 2): for example, in 1975, they were 8.5%, 67.1%, and 24.3%, respectively, while in 1980 there were 7.1%, 28.0%, and 64.9%. The relative numbers returning at ages 4_2 and 5_2 vary within the range 3:1 to 1:3. This introduces another source of variation in marine survival, since fish that stay at sea until age 5_2 are exposed to sources of marine mortality for a longer period of time than those that return earlier.

Because the division into age 4_2 return and age 5_2 return is so variable, we would not expect smolts to predict these numbers any better than they predict total return. The correlation with age 4_2 return ($r = 0.235$, $n = 22$, $F_0 = 1.17$, $P = 0.29$) is weaker than the correlation with age 5_2 return ($r = 0.401$, $n = 21$, $F_0 = 3.64$, $P = 0.07$) (Fig. 8), but neither relationship, on its own, offers strong predictive power.

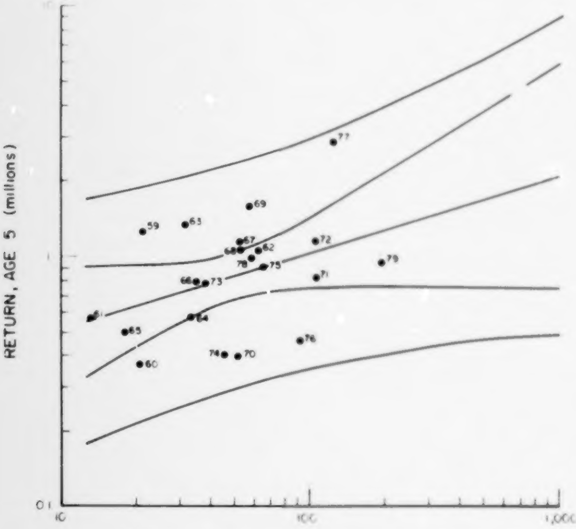

FIG. 8 Age 5_2 return from each brood year, 1959–79, plotted against numbers of smolts. Same format as Fig. 3.

SIBLING RELATIONS

The correlations between returns of different sibling groups from the same brood (jacks, age 4_2 return, age 5_2 return) are much stronger than those between smolt numbers and returns. This is consistent with conclusions of Ricker (1962), Hartt (1980), and Peterman (1982a), that marine mortality is most variable from the time that smolts reach the estuary, and in the 15 mo thereafter. We would not, however, expect these correlations to be high, because the division of the brood into age 4_2 return and age 5_2 return is so unpredictable: for example, an unusually strong return of 4_2's may reflect a strong brood year (and hence predict a strong return of 5_2's) or it may simply indicate a higher than usual proportion returning at age 4_2 (and hence a reduced proportion returning at age 5_2). Returns of jacks and 4_2's from the same brood are positively correlated ($r = 0.647$, $n = 28$, $F_0 = 18.7$, $P<0.001$) (Fig. 9). The correlation between jacks and 5_2's (not shown) was only slightly weaker ($r = 0.476$, $n = 28$, $F_0 = 7.62$, $P = 0.01$). Hence jacks can be used to predict both of these returns of older fish from the same brood. The correlation between 4_2 return and 5_2 return is also statistically significant ($r = 0.586$, $n = 27$, $F_0 = 13.1$, $P<0.002$) (Fig. 10).

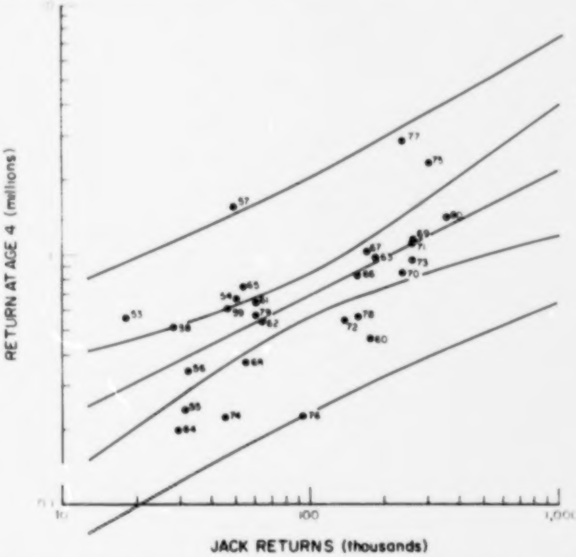

FIG. 9. Age 4_2 returns from each brood year, 1953–80, plotted against jack (age 3_2) returns. Same format as Fig. 3.

Predictions based on sibling returns would be sharpened if the division of a brood into 4_2 return and 5_2 return could be predicted. To see if the division is related to the composition of the parent stock, we selected the 10 years in which the proportion of 5_2's among the spawners was lowest, and the 10 years in which it was highest, and looked at the division of their offspring. The results (Table 5) are entirely consistent with the hypothesis that 4_2's and 5_2's are equally likely to predominate, regardless of parent stock composi-

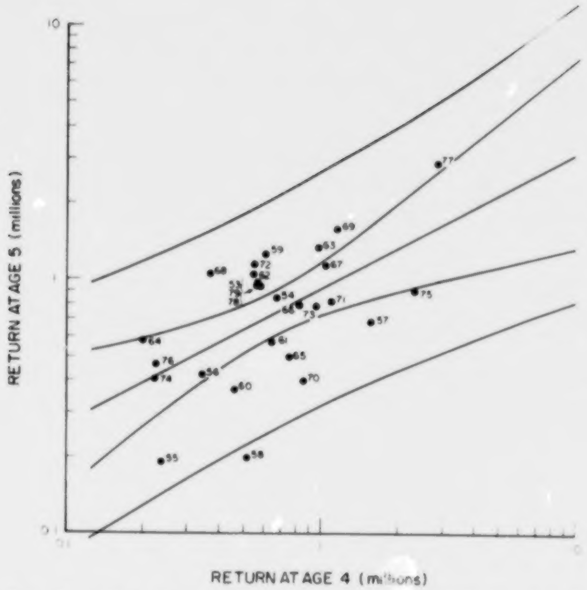

FIG. 10. Age 5_2 returns from each brood year, 1953–79, plotted against age 4_2 returns. Same format as Fig. 3.

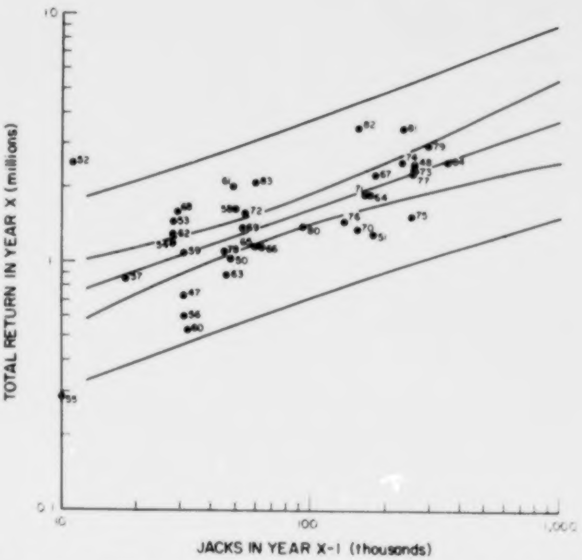

FIG. 11. Total return in each calendar year, 1954–84, plotted against jack returns in the previous year. Same format as Fig. 3, except that the calendar year, not the brood year, is given for each point.

TABLE 5. Spawners aged 5_2 (as a percentage of 4_2's and 5_2's) in Skeena River parent stocks and their progeny, for the 10 brood years with the highest parent percentage and the 10 brood years with the lowest parent percentage, 1940–84.
* indicates progeny with > 50% 5_2's.

Years of highest proportion 5_2			Years of lowest proportion 5_2		
Brood year	Parent	Progeny	Brood year	Parent	Progeny
1968	84	72*	1979	9	59*
1947	78	51*	1984	13	18
1946	76	75*	1956	13	51*
1945	76	32	1940	14	70*
1949	75	36	1960	18	40
1959	75	66*	1961	18	43
1955	71	37	1953	19	61*
1978	74	62*	1963	19	57*
1972	70	67*	1965	21	35
1950	69	24	1952	21	13
Average	74.5	52.2*		16.5	44.7

tion. Nevertheless, Larkin and McDonald (1968) did report a weak correlation between the average ages at spawning of parents and their progeny.

RELATIONS BETWEEN TOTAL RETURN IN A CALENDAR YEAR AND INDICATORS OF ITS COMPONENT AGE—GROUPS

The total return to the Skeena River in a given calendar year is composed of 3_2's (jacks), 4_2's, 5_2's, and a very few 6_2's, 4_3's, 5_3's, and 6_3's. Two of these age-groups, 4_2 and 5_2, almost always comprise 90% or more of the run, and the jacks are of limited commercial importance, so the forecasting problem is essentially that of forecasting the 4_2's and 5_2's.

Let X denote a given calendar year. The 4_2's that return in year X are siblings of the jacks that returned in year X-1, both groups having originated in brood year X-4. It was shown above ($r = 0.647$, Fig. 9) that jacks in year X-1 are a good predictor of 4_2's in year X. Fig. 11 shows that they are equally good as a predictor of the total return in year X ($r = 0.669$, $n = 37$, $F_0 = 28.4$, $P<0.001$), even though the total return includes a component (the 5_2's) from a separate brood year. Possibly, the reason why Fig. 9 does not show a stronger correlation than Fig. 11 is that the age composition is not always determined accurately and this introduces error into the estimate of return of age 4_2 (the ordinate of Fig. 9). In contrast, total return in calendar year X (the ordinate of Fig. 11) is estimated without having to know the age composition.

The 5_2's that return in year X could be predicted by the 4_2's that returned in year X-1 ($r = 0.586$, Fig. 10), or by the jacks that returned in year X-2 ($r = 0.476$), or by the smolt run in year X-3 ($r = 0.401$, Fig. 8), since all of these groups originated in brood year X-5. Curiously, only one of these indicators, the smolt run in year X-3, has a signifi-

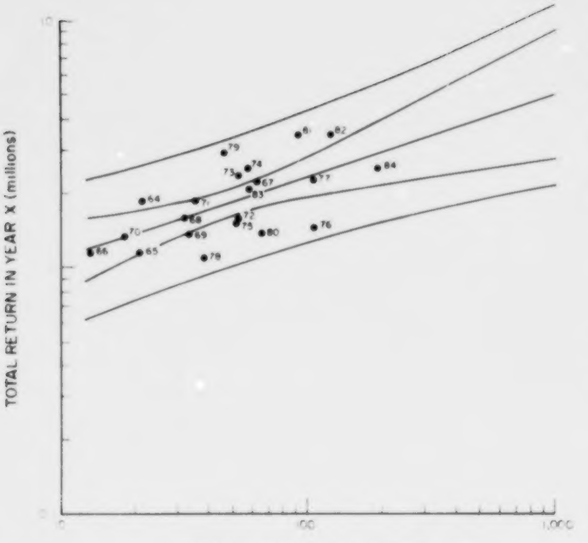

FIG. 12. Total return in each calendar year, 1964–84, plotted against numbers of smolts 3 yr previously. Same format as Fig. 11.

cant correlation with the total return in calendar year *X* ($r = 0.632$, $n = 21$, $F_0 = 12.6$, $P = 0.002$) (Fig. 12), it is possible that even this correlation is just an artifact of comparing two autocorrelated series (total return and smolt numbers) at a fortuitous lag (3 yr). This was investigated by looking at all possible lags; two other strong correlations were found, at lag 0 yr ($r = 0.66$) and lag 7 yr ($r = 0.64$), but biological interpretations for these would be rather farfetched, hence they were not used.

FORECASTING THE TOTAL RETURN IN A CALENDAR YEAR

The simplest possible predictor of total return in a given calendar year is just the historical average. This does not take into account the special conditions of any particular brood or any particular calendar year. Taking the average of log-transformed total returns over the period 1964–84 gives an estimated return of 1.84 million sockeye per year. Assuming that returns in successive years are statistically independent leads to a 95% prediction interval of 0.87 million to 3.90 million. These 95% limits are a factor of 4.5 apart. The 21-yr period 1964–84 was chosen as a compromise; earlier data are less relevant to present-day conditions, but restriction to, say, the five most recent years, would not give a series long enough for reliable forecasting.

Because some autocorrelation is evident in the series for total return, an attempt was made to forecast by fitting a Box–Jenkins (1970) model, again using the 1964–84 data. In all cases this model gave prediction intervals even wider than the one computed above, which assumed independence. Even the factor of 4.5 is much too great for management purposes. The predictor cannot be based on the historical returns alone, some indicator variables must be used as well.

The possible indicators for total return in calendar year *X* have been discussed above. They include numbers of spawners in years *X*-5 and *X*-4, numbers of fry in years *X*-4 and *X*-3, numbers of smolts in years *X*-3 and *X*-2, numbers of jacks in years *X*-2 and *X*-1, and the number of age 4_2 adults returning in year *X*-1. These indicators were used as independent variables in a stepwise regression, with total return in year *X* the dependent variable and all numbers log-transformed. Stepwise regession invariably selected smolts in year *X*-3 and jacks in year *X*-1 as the best indicators, with a coefficient of multiple determination, r^2, of O.568. After taking antilogarithms, the relationship, fitted to data from return years 1964-84, can be written as

$$\text{Predicted total return in Year } X = 3052 \times (\text{smolts in year } X\text{-}3)^{0.213} \times (\text{Jacks in year } X\text{-}1)^{0.224}$$

The multiplicative form of this expression is a consequence of multiple linear regression on log-transformed data. If we think of the smolts as predicting the 5_2's and the jacks as

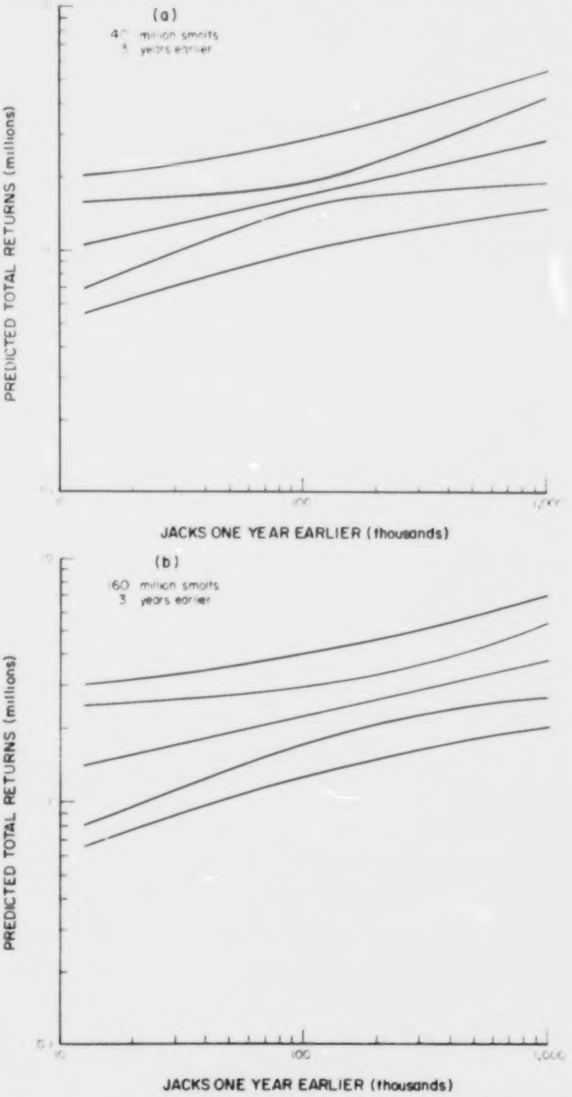

FIG. 13. Two charts from a series of charts that can be used to predict total return in a given calendar year from the number of jacks returning 1 yr prior and the number of smolts migrating 3 yr prior. For explanation, see the text.

predicting the 4_2's, it would make more sense to consider non-linear models that add the smolt and jack terms, instead of multiplying them. Some non-linear models were fitted to the data but no advantage was found over multiple linear regression on log-transformed data.

Multiple linear regression permits simple calculation of confidence bounds for the predictor itself, as well as bounds for the predicted total return, for any given combination of smolt numbers (3 yr before) and jack numbers (1 yr before). These can be summarized in a series of charts, two which are shown in Fig. 13. Pick the chart corresponding to the number of smolts three years prior, pick the abcissa corresponding to the number of jacks returning one year prior, and read from the graph the predicted total return for the current year (the central straight line), a 95% confidence interval for the true value of the predictor (the inner bounds about the straight line), and a 95% prediction interval for the actual return in the current year (the outer bounds). On these charts, the upper 95% prediction bound ranges from about 3 times the lower bound (Fig. 13a, centre) to about 4.5 times the lower bound (Fig. 13b, extreme left), and the factor is less than 4 for most cases of interest, so this forecast method is preferable to the simple historical average. The stepwise regression results indicate that it provides the best pre-season forecast possible, when only the indicators listed above are used.

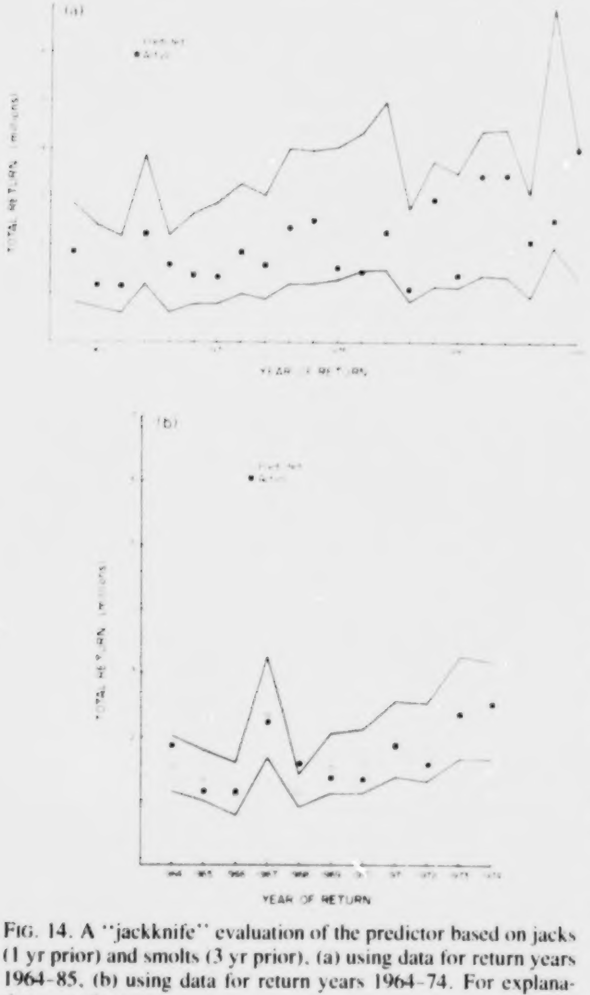

FIG. 14. A "jackknife" evaluation of the predictor based on jacks (1 yr prior) and smolts (3 yr prior). (a) using data for return years 1964–85. (b) using data for return years 1964–74. For explanation, see the text.

The "jackknife" evaluation of the predictor is shown in Fig. 14. In Fig. 14a, the predicted return and 95% prediction bounds for 1964 were found after re-fitting the multiple regression to 1965–85 returns; the predicted return and 95% prediction bounds for 1965 were found after re-fitting the multiple regression to 1964 and 1966–85 returns; and so on, so that each prediction was based on 21 yr of data. While the actual returns are all within the 95% bounds, it is clear that predictions after about 1974 are less precise than those before 1974, and hence the prediction bounds are unnecessarily wide for returns before 1974. Figure 14b shows the same "jackknife" evaluation restricted to the 1964–74 returns and the 95% prediction bounds are much tighter, in many cases less than a factor of 2 apart.

Figure 14a also shows that the average annual return since 1974 is about 1 million fish higher than the average return in the period 1964–74. This increase is attributable to the Development Project. It is likely that the lessened predictability also may be attributed to the Development Project, for one or more of the following reasons. First, changes in population structure induced by the Development Project (e.g., higher proportions of jacks) may mean that each year the forecast is based on a combination of smolt numbers and jack numbers so unlike those experienced in other years that use of the multiple regression predictor is tantamount to extrapolation. Second, the increased stock size *per se* may induce greater variability in marine survival, possibly through changed predation rates in the estuary or elsewhere, as well as through reduced smolt size. Third, limited opportunity with regard to diversification in spawning times and places within the Development Project (particularly in obliging the great majority of the fish to spawn under very uniform conditions both within and among years), may not favour certain population traits that are conducive to high marine survival.

Conclusions

Smolt numbers have proved to be important for pre-season forecasting in other systems (e.g. Fried and Yuen 1987). Together with jack numbers, they provide the best possible pre-season forecast of Skeena River returns, out of all the pre-season indicators considered in this paper. However, at best, this forecast of Skeena returns will be accurate to within a factor of 3 (95% of the time), and this is not precise enough for management purposes. The returns were more predictable before 1974 than they are now.

The precision of the forecasts is limited by the accuracy with which the smolt runs and the various components of the return can be estimated, by the natural variability in survival rates between the time the smolts leave Nilkitkwa Lake and the time they return as adults, and by the natural variability in age at return.

The smolt run estimates have acceptably small coefficients of variation, and there is not much that is cost-effective that could be done to improve the smolt enumeration program. Larger samples and around-the-clock sampling would give only a marginal improvement. It would, however, be useful if an experiment could be designed, as a supplement to holding experiments, to measure the mortality of tagged smolts in Nilkitkwa Lake, as this was assumed to be negligible or at least consistent day-to-day and year-to-year. Experiments are also needed to test the possibility that tagged fish attract predators and thus suffer higher predation in the lake than other smolts.

An important limiting factor in the enumeration of returning adults is uncertainty as to the size of the southeast Alaskan catch. This catch has increased in recent years and may well explain some of the unpredictability of returns since 1974, even though our data were adjusted for Alaskan catches whenever possible. Forecasts should improve as more complete Alaskan data become available. Another limiting factor is the reliability of the age composition estimate, although this was not used when forecasting total returns in a given calendar year. Further studies should be done to ensure that age composition estimates are based on representative samples, and to assign levels of confidence to them.

Pre-season forecasts are not likely to be reliable until more is known about the factors affecting survival of juveniles in the river and the estuary, and sub-adults at sea, and the factors determining age at return. It may be that the Development Project actually is unwittingly selecting for freshwater survival at the expense of marine survival, in which case the returns will continue to become more and more unpredictable. It would also be worthwhile to investigate such factors as competition with pink salmon (*O. gorbuscha*), and the behaviour of predators in the estuary in response to increasing numbers of juveniles. It may be that accurate preseason forecasts will not be possible until there is better determination of offshore and coastal migration patterns, age composition, and survival rates of the Skeena and spatially associated stocks. It is quite conceivable that to acquire these data fisheries managers must pay the price of new high seas investigations. Age at return of Skeena River stocks cannot be predicted from either the age composition of the spawners or the mean size of the smolts, and it is possible that it, too, is strongly influenced by environmental factors at sea.

The mean size of late-run smolts has declined since the onset of the Development Project, presumably in response to increased numbers. While there is no year-to-year response of mean size to variations in density, the response may be buffered in the short term, with the gradual decline in size being the response to a number of years of relatively high density. The fry-to-smolt survival rate appears to be remarkably high, often more than 50%, even allowing for a possible upward bias in the smolt estimates as a result of tagging mortality and a possible downward bias in the fry estimates as a result of uncounted or unaccountably successful lake spawners.

Acoustic enumeration of migrating smolts (Fried and Yuen 1987) may ultimately prove to be more cost effective than the present mark-recapture method. Should a change to acoustic enumeration be proposed, it would be imperative to continue mark-recapture enumeration in parallel for at least 3 years to calibrate the acoustic estimates against the mark-recapture estimates and thus ensure the continuity of the data series. Acoustic surveys of pre-migratory juveniles in the lake (Mathisen and Smith 1982) looked at the population from a different point of view and could be used to supplement, but not supplant, enumeration of migrating smolts.

We see four important reasons why the smolt enumeration program should continue. First, it is the best means of measuring freshwater growth and survival of Development Project stocks. The smolt data will, for example, give the first warnings if production exceeds the carrying capacity of Babine Lake. Second, future studies of the factors affecting survival rates in the river, estuary, and ocean will require "base numbers" obtained by reliable estimates of juvenile production. Third, the smolt estimates are an important component of pre-season forecasts. While good preseason forecasts may not be possible until more is known about marine survival and the factors affecting age at return, we believe that smolt numbers will continue to be an important component of forecasts when these parameters are included. Fourth, there is a wide interest in the dynamics of Babine and Skeena stocks among fisheries managers, government research agencies, and researchers at universities, and such comprehensive, long-term data series exist for few other sockeye salmon stocks. Only long-term series, spanning several decades, can show long-term trends or the effects of interventions such as the Development Project. At Babine Lake, unique expertise has been developed to carry out the smolt enumerations consistently from year to year, and the value of this series will increase in the years ahead.

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Sea Surface Temperature and the Pre-Season Prediction of Return Timing in Fraser River Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

Blackbourn, D. J. 1987. Sea surface temperature and the pre-season prediction of return timing in Fraser River sockeye salmon (*Oncorhynchus nerka*), p. 296–306. *In* H.D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

A simple temperature-displacement model is proposed to account for the annual variation in run timing in Fraser River sockeye salmon (*Oncorhynchus nerka*) stocks. Results of the application of the model show that sea surface temperature (SST) in the central Gulf of Alaska is positively related to annual return timing for seven stocks of Fraser River sockeye and alone accounts for between 30 and 94% of the variation in timing from 8 to 31 years of data. That part of the Gulf and time of year showing the strongest statistical relationship vary in an apparently logical manner from stock to stock. Predictions of the general utility of the model are supported by timing data from four stocks of sockeye returning to the northern Gulf of Alaska. The consequences of using specific areas of the Gulf in this method are discussed, with the 1985 Fraser sockeye run as an example.

Résumé

Blackbourn, D. J. 1987. Sea surface temperature and the pre-season prediction of return timing in Fraser River sockeye salmon (*Oncorhynchus nerka*), p. 296–306. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Un modèle simple température-déplacement est présenté pour expliquer la variation annuelle du moment de la remontée des stocks de saumon nerka (*Oncorhynchus nerka*) du fleuve Fraser. L'application du modèle a permis de noter que la température de la surface de la mer dans la partie centrale du golfe de l'Alaska présentait une corrélation positive avec le moment de la remontée annuelle de sept stocks de saumon nerka du fleuve Fraser et permettait à elle seule d'expliquer de 30 à 94 % de la variabilité du moment de la remontée ceci pour de 8 à 31 années de données. La partie du golfe et le moment de l'année présentant la plus importante relation statistique semblent varier de façon logique entre les stocks. Les prévisions relatives à l'utilité générale du modèle sont appuyées par les données sur le moment de remontée de quatre stocks de saumon nerka revenant dans la partie nord du golfe de l'Alaska. On traite des effets de l'utilisation de zones précises du golfe en prenant comme exemple la remontée du saumon nerka de 1985 dans le fleuve Fraser.

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Introduction

Knowledge of the long-term mean date of return timing for each Fraser sockeye stock has been an integral part of sockeye management by the International Pacific Salmon Fisheries Commission for many years (Henry 1961; Killick 1955; Verhoeven and Davidoff 1962). Interannual variation in run timing of major stocks can be an important element in the success of the annual fishery management plan. Study of the effects of environmental factors on return timing has included analyses of correlations between these variables. Preseason prediction of the peak timing of the major Fraser sockeye stocks has been a feature of Commission management since 1977 (IPSFC Annual Reports, 1978 through 1984).

A simple model was proposed early in my investigations and formed the basis of further analyses. In this paper I report on the results of comparisons between sea surface temperatures and return timing of several Fraser River sockeye stocks. Results will also be given of the extension of the model to other sockeye stocks in the Gulf of Alaska. Some implications to fisheries management of the use of the method will be discussed.

A Temperature-Displacement Model of Annual Variation in Run Timing of Sockeye Salmon

DEVELOPMENT OF THE MODEL

Gilhousen (1960) and Killick and Clemens (1963) postulated that variation in the run timing of Fraser River sockeye could be affected by sea surface temperature during their last year. Gilhousen (1960) postulated that the effect of temperature on the fish was physiological, and either (a) direct, presumably on the speed of migration, or (b) indirect, by causing annual variation in the latitudinal distribution of the sockeye. The latter would in turn cause variation in their maturation rate due to exposure to latitudinally varying photoperiod. Killick and Clemens (1963) also implied a physiological effect of latitudinal displacement on run timing due to temperature variation. However, the latter authors thought that cold temperatures in the centre of the Gulf of Alaska might lead to the southward movement of Fraser sockeye into an area of invariably greater food supply which, in turn, might lead to the early onset of migration via increased growth and subsequent early maturation. The opposite tendencies were thought likely to be the result of warm temperatures in the central Gulf.

I considered that both of the foregoing physiological theories had the weakness that they were too specific to Fraser sockeye. Such theories implied that the effect of temperature on the travel speed or maturation of returning sockeye would be likely to have the opposite effect on sockeye returning to the southeastern edge of the Gulf compared to those returning to the northern edge of the Gulf. Of course, this difference is only a theoretical weakness when both sets of stocks are considered together. A simpler, more general, temperature theory was produced based upon the effects of displacement itself, rather than on its possible physiological effect on the onset of migration or on swimming speed. The theory was based on considerations of variation in ocean temperature alone. Some of the general theories of salmon migration have been concerned with the effect of such environmental factors as ocean currents (Royce et al. 1968) or magnetic fields (Quinn 1982). However, at present, predictive models of the interannual variation in salmon run timing cannot be based on ocean currents or magnetic fields due to the scarcity of annual data for these and most other environmental factors in the open ocean.

It is arbitrarily assumed in this model that the horizontal movements of sockeye prior to the last marine winter have negligible interannual variation. This simplifying assumption was borne out by the results of some preliminary analyses. Perhaps the temperature-sensitive displacement is time-dependent or begins only at a certain state of maturity. It is further assumed that the movements of the sockeye during and after the last marine winter fall into two types: (a) relatively slow "non-directed" migration occupying the first several months in response to seasonal changes in surface temperature or in the boundaries of ocean " domains", such as those discussed by Favorite et. al. (1976) and (b) later, relatively rapid, "directed" migration toward the home stream, largely independent of the boundaries of ocean parameters, and lasting no more than about 2 months. The latter independence is supported by a study of Bristol Bay sockeye migration (French and Bakkala 1974). The model assumes that interannual variation in salmon return timing is determined sometime between November and July for various stocks during period (a) above.

The various species of salmon have different centres of distribution in the North Pacific (French et. al. 1976; Takagi et. al. 1981). There are also differences between the centres of distribution of various stocks of one species of salmon from different broad geographical areas, e.g., Western Alaskan sockeye and British Columbia sockeye (French et. al. 1976). These large-scale distributional differences may be, in part, due to optimum ranges of temperature. With no direct supporting evidence, I have assumed that each *stock* of sockeye will have an optimal though not exclusive area of distribution and that it will attempt to stay within some fairly narrow, stock-specific optimum range of sea surface temperature within that area. The location of this optimum temperature range within the optimum areas will change with the seasons: northward (or northwestward in the eastern Gulf of Alaska) in spring and summer; and in the reverse direction in fall and winter. The centres of sockeye abundance will change in concert with temperature changes. The position of the optimum temperatures within the optimum areas in any one season will also vary from year to year. Therefore the seasonal position of the salmon will also show interannual variation.

This simple theory assumes that each year within a general area of stock-specific distribution, the position of the maturing salmon prior to stage (b) — the directed homeward migration — will be determined by the position of the optimum temperatures at that time. For most stocks of sockeye, stage (b) will begin in the spring when ocean temperatures are largely determined by conditions during the prior winter. After an unusually warm winter, the optimum temperatures for a particular stock will be further north than usual. As a result, the salmon of that stock may also be further north than usual in the spring (see Fig. 1).

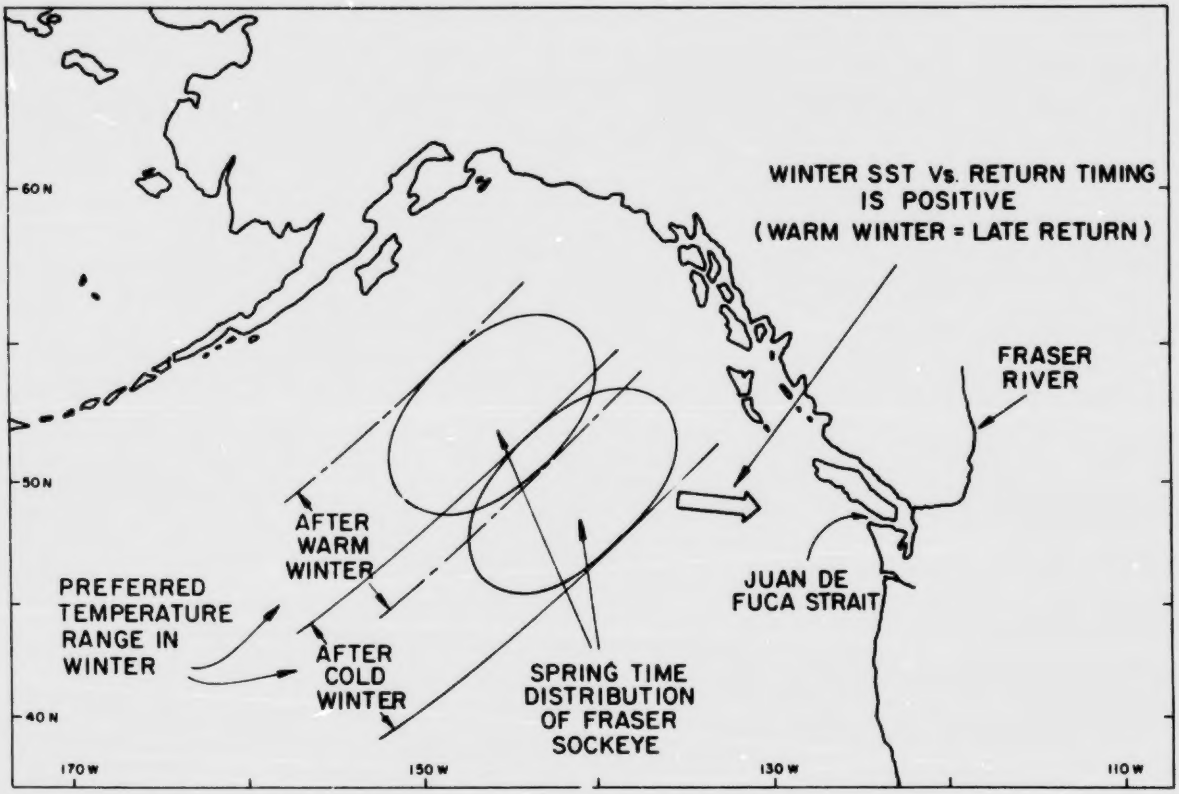

FIG. 1. A simple temperature-displacement model of the return timing of Fraser River sockeye salmon.

Fraser River sockeye stocks return to the homestream in an eastward or southeastward direction (French et. al. 1976). According to the model, very warm winter and spring sea surface temperatures should result in the maturing adults being appreciably further from the Fraser than usual, before they begin their directed homeward migration. It is also assumed that the onset of phase (b) and their speed of migration in either phase (a) or (b) is little affected by temperature, and so the warm temperatures during phase (a) should result in late return timing for Fraser sockeye. Conversely, unusually cold temperatures during phase (a) should result in the displacement of Fraser sockeye to the south and their subsequent early return to the river.

This "displacement" model predicts that salmon returning northward to their home stream will show the opposite relationship between the date of peak return timing and sea surface temperature during the non-directed phase of migration in the last year. Warm temperatures experienced by salmon stocks returning to the north of their winter distribution should cause them to show early return timing.

The model was tested by comparing sea surface temperatures in the Gulf of Alaska with the return timing of various stocks of Fraser sockeye with from 8 to 31 years of data. Testing of the general model was broadened by examination of timing in four sockeye stocks with origins in the northern boundary of the Gulf of Alaska and one originating south of the Fraser. Although the model was developed for sockeye it has also been applied to other species of Pacific salmon (Blackbourn 1984).

Application of the Model

METHODS

Sockeye Timing Data

Return timing is here defined as the peak day of numerical abundance of a stock of Fraser sockeye in outer Juan de Fuca Strait. Gaps in the data (Table 1) result when some sockeye stocks are not numerous enough every year for their timing to be clearly distinguished from that of other concurrent stocks (Henry 1961). Also, in some recent years it has not been possible to specify a peak timing date in Juan de Fuca Strait for several stocks because major portions of the runs returned to the Fraser via another route (Johnstone Strait).

The peak dates (Julian day) (Table 1) were calculated by a variety of methods. These methods changed over the years from simple estimates based on frequent, terminal commercial fisheries in the Fraser River in the 1950's and 1960's to those made by comparisons of graphs of catches by time period from a mixture of test and commercial fishing in Juan de Fuca and Georgia Strait in the 1970's; and by complex run reconstruction methods in the most recent years. Dates of peak timing in the Fraser River and southern Georgia Strait have been adjusted to Juan de Fuca Strait timing with a knowledge of the behaviour of individual stocks by the subtraction of 4 or 5 days from the river dates and 3 days from Georgia Strait dates. For the few years when multiple peaks were apparent, a calculated day of passage of 50% of the

TABLE 1. Adjusted date of peak timing (Julian Day) of Fraser sockeye to outer Juan de Fuca Strait.

Return Year	Early Stuart	Pitt River ($^5/2$)	Horsefly River	Chilko River	Stellako River	Adams River	Weaver Creek
1950	—	—	—	—	—	233 D[b]	
1951	—	—	—	209	—	225	
1952	—	205		207	—		
1953	187	205	203	205	204		
1954	184	198		208	220	240 D	
1955	183	204		212	217	229	
1956	—	203		213	209		
1957	188	202	212	216	219		
1958	195	208		223	239	244 D	
1959	187	217		217	—	235	
1960	—	204		217	—		
1961	185	205	207	210	212		
1962	183	206		211	217	241 D	
1963*[a]	182	203		204	215	222	
1964	—	207		214	213		
1965	183	206	207	209	216		
1966	183	212		211	214	234 D	
1967	191	204		211	223	232	
1968	—	203		211	211		
1969	184	202	204	205	213		225
1970	180	207		216	225	236 D	—
1971	185	208		211	225	230	—
1972	—	204		217	211		223
1973	185	210	210	214	214		231
1974	183	209		215	214	234 D	232
1975	182	206		207	211	228	—
1976	—	200		214	216		223
1977	183	206	206	—	—		229
1978	180	199		216		234 D	236
1979*	182	—		216		217	227
1980	186	—		221			
1981	185	—	218	—			
1982	185	—		219		231 D	
1983	—	—		—		—	
1984	—	—		217		—	
1985	—	—	222	—			

[a]* — Data not included in all analyses (see text).

[b]D — Adams "dominant" cycle.

stock was used as the peak date. There is no objective estimate of the error involved in calculating the peak dates.

Environmental Data

Sea surface temperature (SST) data from B.C. Lighthouse stations were obtained from the Institute of Ocean Sciences, Sidney, B.C. in published and unpublished form (e.g. Giovando 1983). Open ocean sea surface temperature data from ships were obtained from Dr. D. McLain, N.M.F.S., Monterey (unpublished) and from ships, buoys, and satellites from the publication *Oceanographic Monthly Summary* (U.S. National Weather Service, N.O.A.A., Washington, D.C.). The latter SST data were averaged by month over 5° squares of latitude and longitude ('Marsden' squares in Fig. 2).

It was assumed from the results of I.N.P.F.C. tagging during the 1960's that the position of Fraser sockeye in their last marine spring before return would be slightly west of the centre of the Gulf of Alaska at about 53°N and 150°W with perhaps the earlier returning stocks distributed farther to the south (French et. al. 1976).

Analysis

SST data from the above area of the Gulf and from the B.C. coast were compared to the annual peak return timing of Fraser sockeye stocks to Juan de Fuca Strait by simple and multiple least squares regression analysis.

From my (unpublished) analysis of the relatively few I.N.P.F.C. tagged Fraser sockeye which are identified as to stock of origin, certain 5° squares of SST data were initially chosen for comparison with timing data for particular stocks of sockeye. First, mean monthly temperatures by Marsden square were correlated to timing. Then temperature data for adjacent months and areas were pooled and their averages compared with run timing. The largest of the resulting correlation coefficients served to identify the time-area combination yielding maximum explained variability in run timing.

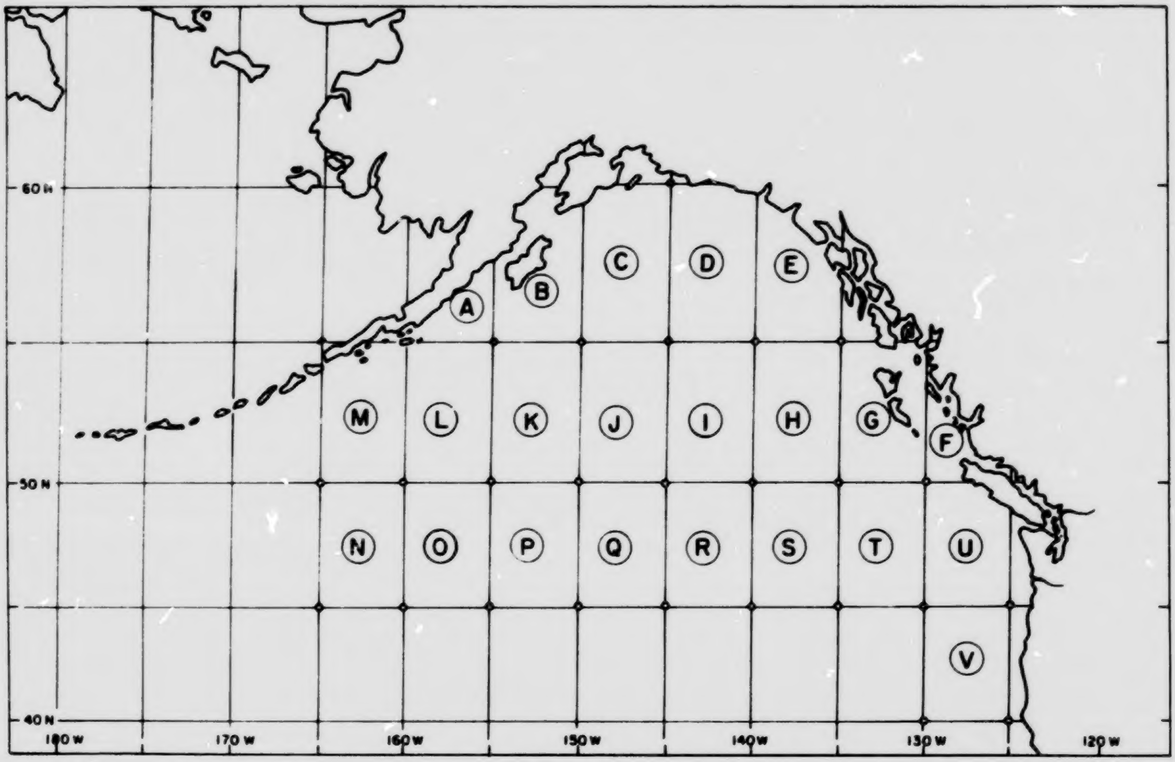

FIG. 2. Author's designation of 5° (Marsden) squares of latitude and longitude.

Results and Discussion

A. SEA SURFACE TEMPERATURE (SST) AND FRASER SOCKEYE TIMING

The hypothesis was based on very general distributional data, but insufficient tagging data exist on Fraser sockeye salmon in general, or in any particular year, to be sure of their position in the Gulf of Alaska. We know least of all about their distribution during fall and winter (French et. al. 1976). In addition, most of the I.N.P.F.C. tagging occurred during the 1960's, a period of moderate surface temperatures when compared to the cool 1970's and warm early 1980's (Table 3). For these reasons, when it was found that much higher coefficients between SST and timing occurred at a time and place different from that originally chosen in the initial tests, it was felt to be justified on practical grounds that the time and area of highest coefficient was subsequently used in analysis and prediction.

Time and area(s) of highest correlation coefficient between sea surface temperature in the last marine year and the peak return timing to outer Juan de Fuca Strait differed for the adults of seven stocks of Fraser River sockeye (Tables 2 to 4).

The results shown in Tables 2 to 4 and Fig. 3 are consistent with the predictions of the model in that:

a) The sign of the relationship between SST and return timing is positive and statistically significant for these stocks which return to the southeast. From 30 to 94% of the variation in timing is accounted for by SST.

b) For each stock the SST period most highly correlated with run timing occurred well before it returned to the coast.

c) The SST area of highest correlation for each stock was fairly restricted to up to two or three adjacent 5° squares. (Detailed results not shown — D. Blackbourn — in progress).

The distribution of the areas of highest correlation coefficients for four of the stocks (Fig. 3) indicates that they form a fairly consistent pattern, which reflects the pattern of return timing for those stocks. For example, the earliest returning stock (the Early Stuart Lake group) has its SST area to the southwest of the late stock from Adams River (dominant cycle only), with the SST areas of the midsummer stocks from Horsefly and Chilko rivers lying more or less in between them. The difference between the SST areas for Horsefly and Chilko sockeye will be further discussed later. Similarly, the SST period for the Early Stuart stock is earlier than those for the midsummer stocks (Tables 2 to 4 and Fig. 3), which in turn are earlier than those for the Adams River sockeye.

In other studies, sea level pressure and its derivatives such as indices of surface transport have been compared to Fraser sockeye run timing. Likewise, several environmental factors from B.C. coastal areas have been compared with run timing in simple and multiple regression analyses (D. Blackbourn, in progress). None of these factors account for a significant amount of variation in run timing (results not shown) and in most cases such factors do not account for much variation in addition to that accounted for by SST alone.

TABLE 2. Time and area of highest correlation coefficient between sea surface temperature (SST) in the last marine year (Fig. 2) and peak Julian Day of return timing of various stocks of adult Fraser sockeye salmon (Table 1) to Juan de Fuca Strait.

Stock	Years of data	Mean peak timing Julian Day	Strongest relationship with SST		
			Time	Area(s)	Correlation Coefficient(r)
Early Stuart	24	185	Dec. (Yr-1)	Q	0.67**[a]
Pitt River ($^{5}/_{2}$'s)	27	205	Dec. (Yr-1)	J & K	0.55**
Horsefly River	9	210	Dec. to Jan.	K	0.97**
Chilko River[b]	31	213	Jan. to March	I	0.67**
Stellako River[b]	22	216	Dec. to March	J	0.70**
Adams River 1950 Cycle "Dominant"	9	236	Jan. to July	D	0.94**
Adams River 1951 Cycle "Sub-dominant"[b]	7	227	Jan. to July	E	0.56[c]
Weaver Creek	8	228	April to May	G	0.84**

[a] * — Significant to P 0.05 level;
** — Significant to P 0.01 level.

[b] 1963 data excluded (see text).

[c] 1979 data included — if 1979 data excluded $r = 0.85$* (see text).

TABLE 3. Average sea surface temperature (degrees celsius) for various periods and areas of the Gulf of Alaska (see Tables 1 and 2 and Fig 2).

Area Period	Q December (Yr-1)	K Dec. to Jan.	I Jan. to March	D Jan. to July
1950	8.62	5.43	5.58	6.27
1951	7.85	4.59	4.86	—
1952	8.10	4.97	4.87	—
1953	7.97	4.73	5.23	—
1954	7.29	4.84	5.24	7.38
1955	7.57	4.99	5.71	7.24
1956	8.03	4.91	4.81	7.51
1957	8.41	5.23	5.51	7.54
1958	9.91	5.83	6.54	8.94
1959	7.72	5.23	5.92	8.30
1960	8.17	4.89	5.61	7.27
1961	7.14	4.95	5.49	8.07
1962	8.72	5.32	5.75	7.46
1963	7.67	5.28	6.00	8.20
1964	7.71	5.30	5.62	7.52
1965	7.70	4.78	5.03	6.07
1966	7.88	5.13	5.25	6.74
1967	8.16	4.81	5.05	5.39
1968	7.30	4.87	5.13	7.39
1969	6.98	4.43	4.19	6.17
1970	7.37	5.25	5.84	6.98
1971	8.04	5.32	5.20	5.85
1972	8.05	4.85	4.73	5.53
1973	8.40	5.07	5.24	6.16
1974	7.46	5.09	5.06	6.36
1975	7.82	4.99	4.97	6.08
1976	7.40	4.61	5.07	6.57
1977	7.51	4.90	5.78	7.46
1978	7.04	4.42	5.70	6.51
1979	8.37	5.46	5.85	6.88
1980	8.23	5.13	5.74	6.75
1981	7.91	5.55	6.30	7.44

TABLE 3. (*Continued.*)

Area Period	Q December (Yr-1)	K Dec. to Jan.	I Jan. to March	D Jan. to July
1982	7.41	5.09	5.69	6.45
1983	7.84	5.26	6.01	7.47
1984	8.04	5.74	6.56	7.73
1985	7.71	5.85	6.13	6.58

TABLE 4. Regression equations for sea surface temperature and return timing for four stocks of Fraser sockeye salmon (see Tables 1 to 3).

				Regression equation		
Stock	Time	Area	*n*	*r*	*a*	*b*
Early Stuart	Dec. (Yr-1)	Q	24	0.67**[a]	157.37	3.47
Horsefly River	Dec. to Jan.	K	9	0.97**	137.70	14.28
Chilko River	Jan. to March	I	31	0.67**	180.91	5.97
Adams River (1950 Cycle)	Jan. to July	E	9	0.94**	202.93	4.77

[a]** Significant to $P<0.01$ level.

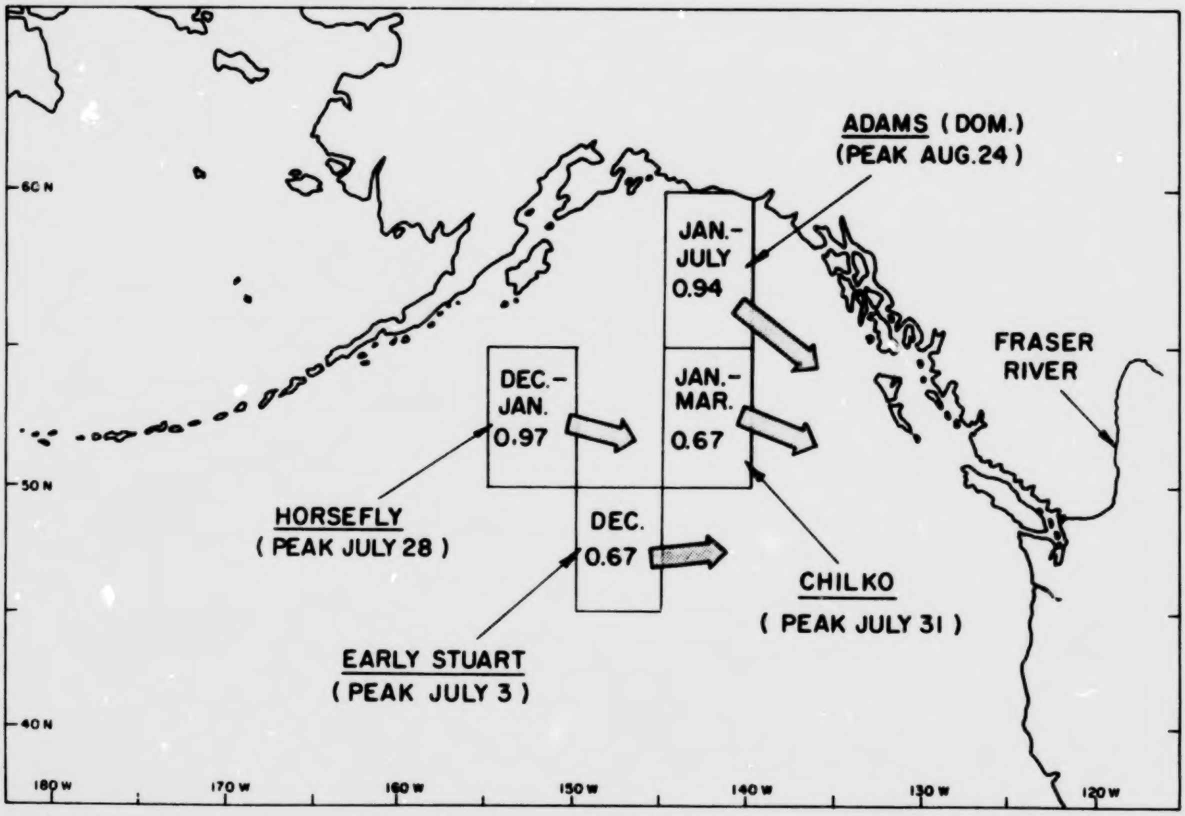
ADAMS (DOM.)
(PEAK AUG.24)
JAN.-
JULY
0.94
FRASER
RIVER
DEC.-
JAN.
0.97
JAN.-
MAR.
0.67
DEC.
0.67
HORSEFLY
(PEAK JULY 28)
CHILKO
(PEAK JULY 31)
EARLY STUART
(PEAK JULY 3)
60 N
50 N
40 N
180 W
170 W
160 W
150 W
140 W
130 W
120 W

FIG. 3. Areas and times of highest correlation coefficient between sea surface temperature and return timing of various stocks of Fraser River sockeye.

Therefore, it seems likely that useful predictions of run timing in Fraser sockeye will, in future, centre largely on the use of SST from the central Gulf of Alaska, as has been the case over the past several years (IPSFC Annual Reports 1978 through 1984). In some years such as 1963 and 1979 (see Table 1) this method would have given highly anomalous predictions for all (1963) or some (1979) stocks of Fraser sockeye (and see below). These past anomalies are only partly explicable (D. Blackbourn, in progress) and such events can certainly happen again.

Since the prediction of Fraser sockeye run timing began in 1978 the results have been generally good. However, the

TABLE 5. Time and area of highest correlation coefficient between sea surface temperature (SST) in last marine year (Fig 2) and peak return timing of various (non-Fraser) stocks of adult sockeye in the Gulf of Alaska.

Stock	Years of data	Strongest relationship with SST			Source of timing data
		Time	Area(s)	Correlation coefficient (r)	
Chignik River					Conrad (1984)
Black Lake	5	March	L	−0.95**[a]	
Chignik Lake	5	Feb.-March	H & I	−0.99**	
Upper Cook Inlet	18	April April-June April—June	S I J	−0.48* −0.42 −0.42	A. Kingsbury & C. Meacham (pers. comm.)[b]
Copper River	5	April April	H I	−0.95** −0.95**	Merritt & Roberson (1983)
Skeena River (Pinkut-Fulton)	13	May	F	−0.78**	R. Kadowaki & P. Starr (pers. comm.)[c]
Quinault River	10	Dec.-Feb.	K	+0.93**	T. Cooney & M. McBride (pers. comm.)[d]

[a] * — Significant to $P < 0.05$ level;
** Significant to $P < 0.01$ level.

[b] Alaska Dep. of Fish & Game, Commercial Fisheries Division,
333 Raspberry Rd., Anchorage, Ak 99502, USA.

[c] Dep. Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Hammond Bay Rd. Nanaimo, BC. V9R 5K6

[d] Quinault Indian Nation, P.O. Box 189, Taholah, WA 98587, USA.

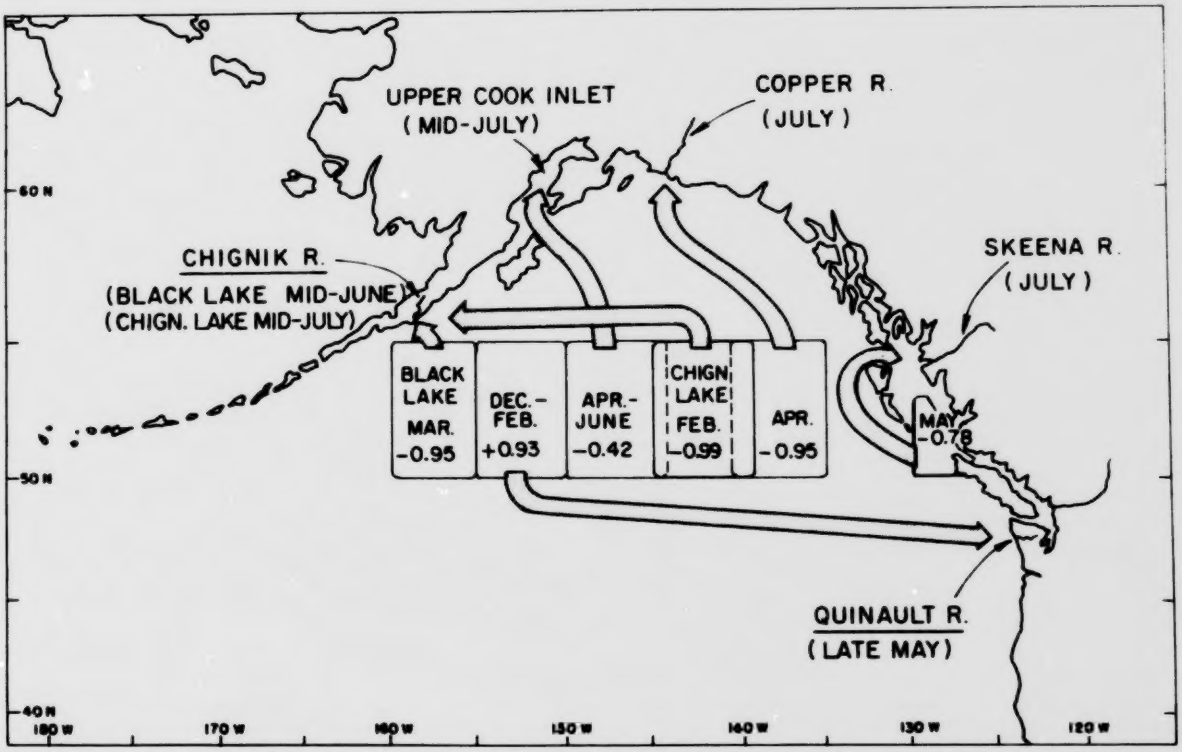
UPPER COOK INLET
(MID-JULY)
COPPER R.
(JULY)
CHIGNIK R.
(BLACK LAKE MID-JUNE)
(CHIGN. LAKE MID-JULY)
SKEENA R.
(JULY)
BLACK LAKE
MAR.
-0.95
DEC.-FEB.
+0.93
APR.-JUNE
-0.42
CHIGN LAKE
FEB.
-0.99
APR.
-0.95
MAY
-0.78
QUINAULT R.
(LATE MAY)
60 N
50 N
40 N
180 W
170 W
160 W
150 W
140 W
130 W
120 W

FIG. 4. Areas and times of highest correlation coefficient between sea surface temperature and return timing of various (non-Fraser) sockeye stocks in the Gulf of Alaska.

accuracy of prediction for Early Stuart stockeye timing has been poor for the last few years and more variable than the observed timing data. In other Fraser sockeye stocks the predicted peak date has nearly always been on the same side of the long-term average as the observed peak date, and for most stocks and years within about 2 days of the latter. The largest anomaly of recent years occurred in 1979 when both the Chilko and Adams stocks were predicted to return later than average. Chilko sockeye did return late, but Adams sockeye were extremely early (Table 1). The use of SST data from any part of the northern Gulf of Alaska would not have given a more accurate prediction for Adams sockeye in 1979.

B. SEA SURFACE TEMPERATURE (SST) AND RETURN TIMING IN OTHER SOCKEYE

Table 5 and Fig. 4 show that run timing in sockeye returning to the Quinault River, Washington is similar to early and midsummer Fraser stocks in that it is significantly and positively related to SST in the northwest Gulf of Alaska in winter. However, this stock returns to the coast earlier (late May) than any Fraser sockeye. Two other early stocks which return in June and July, Great Central Lake, and Lake Washington sockeye, also show a positive relationship between run timing and SST in the northwest Gulf although the coefficients are not statistically significant in these latter two cases (results not shown).

Table 5 and Fig. 4 show results consistent with the prediction of the displacement model in that run timing of sockeye returning northward in the Gulf of Alaska to Chignik River, Upper Cook Inlet, Copper River, and the Skeena River is negatively correlated with SST. Several authors have shown negative relationships between SST and run timing in salmon from Western Alaska (Fujii 1975; Nishiyama 1977; Burgner 1980; Mundy 1982). These results also imply that "physiological" models of the effect of temperature on run timing would have to incorporate very different responses for northern sockeye stocks compared to those from the Fraser River.

The SST areas for Chignik sockeye timing data are in general not too far from the areas in which Chignik fish were tagged in the 1960's (tagging data from C. Harris, Fisheries Research Institute, University, Washington, Seattle, Wash. USA 98195, personal communication). The SST areas for Chignik run timing data from the 1960's (Dahlberg 1968) are A, B, J, and R in Fig. 2 (detailed results not given). Figure 4 shows that the SST areas for Black Lake and Chignik Lake sockeye of the Chignik group are fairly widely separated. The latter data are from the years 1978–82 (Conrad 1984). Presumably only the accumulation of more data will enable us to be sure if this spatial separation accurately reflects the apparent influence of SST on run timing in these two substocks. However, the mean peak timing of Black Lake sockeye is about a month earlier than that of Chignik Lake sockeye, so perhaps the separation may bear some relationship to the relative distribution of the two stocks. Some returning Black Lake sockeye are taken in coastal fisheries to the north of the Chignik River (S. Marshall, Alaska Dept. of Fish and Game, Commercial Fisheries Division, 333 Raspberry Rd, Anchorage, Alaska 99502, USA. personal communication). This does not rule out the possibility that these sockeye are distributed to the south and in or near Area L in March (Table 5), since it is known that adult salmon may "overshoot" their natal stream during migration (Blackbourn 1984; French et al. 1976). Owing to the absence of reports on the oceanic distribution of the other two Alaskan sockeye stock groupings (Upper Cook Inlet and to Copper River), SST areas could not be compared to their actual distribution in the Gulf (Table 5 and Fig. 4).

It is certain, however, that the area of highest coefficient for Skeena River sockeye (Pinkut and Fulton stocks) seen in Table 5 and Fig. 4 is more at variance with I.N.P.F.C. tagging data than is the case for most stocks and is different from the known direction of entry of many of these sockeye to the first fisheries, i.e. from the west and northwest. On the other hand there is little data with which to directly confirm or refute the possibility that SST in the Queen Charlotte Sound area to the south of the Skeena River determines the eventual migration behaviour of Skeena sockeye. This result might leave the Fishery Manager who wishes to predict run timing in this stock in a dilemma, for SST data from an area in the central Gulf (say area I in Fig. 2) would have accounted for only about half of the variation in Skeena sockeye run timing from 1970 to the present compared to predictions from SST data from the coastal area or from coastal stations. Of more importance to the manager is the fact that the latter difference would have been even greater in years of extreme run timing in Skeena sockeye. The Skeena sockeye timing data were taken from the test fishery and from run reconstruction. The latter is partly calculated from the former, and gives similar results (Table 5).

C. THE PREDICTION OF RUN TIMING FROM GENERAL AND SPECIFIC SST AREAS

Table 1 shows that since 1953 and prior to 1985 there were 8 years of peak run timing data for Horsefly river (Fraser) sockeye. This contrasts with 31 years of data over a similar period from another midsummer Fraser stock, that from Chilko River. The SST area for Horsefly sockeye is area K in December and January, and that for Chilko sockeye is area I, from January to March (Fig. 2). It was known in advance that the dominant Fraser sockeye stock in 1985 would return to the Horsefly River whereas Chilko sockeye would be relatively few in number.

In many years, predictions of timing made from area K or I would have been very similar (Tables 1 and 3). However, area K contained a very warm SST anomaly in December 1984 and January 1985, whereas by March and April 1985 the SST in area I was only slightly warmer than average. Since a prediction of Horsefly timing in 1985 from area K would have been for a run much later than any on record, a compromise was made prior to the season. The predictions from three SST areas, (K, I, and S), were combined, as all had a strong statistical relationship with Horsefly timing data. The results of these predictions can be seen in Table 6. The previous long-term average Horsefly peak timing was July 26. The final combined prediction was for August 1 and the prediction from the "Horsefly" area (K) alone was for a peak on August 7. The actual 1985 peak occurred on August 9, more than a week later than the official prediction and was the latest timing on record. The 1985 Horsefly sockeye run was also the largest since 1913 and larger than predicted. Although the difference between correlation coefficients of

TABLE 6. Predictions of 1985 Horsefly River sockeye timing made from sea surface temperature (SST) in two areas of the Gulf of Alaska.

	Corr. coeff. (*r*)		Horsefly Peak timing to Juan de Fuca St.			
Areas of Gulf of Alaska (see Fig. 2)	vs. Chilko Timing ($N = 31$)	vs. Horsefly Timing ($N = 8$)	1985 Prelim. Prediction	1985 Final Prediction	1985 Observed Timing	Average Timing
SST in Area K (Western)	0.53**[a]	0.94**	Aug. 7	Aug. 1	Aug. 9	July 26
SST in Area I (Central)	0.65**	0.87**	July 29			

[a] ** Significant to $P<0.01$ level.

0.87 and 0.94 is small, the practical outcome of using one or the other was very large in 1985 (Table 6). The need for accurate prediction of run timing is particularly great when there is considerable doubt about stock abundance. From this example it seems not unreasonable to use relatively restricted areas for each stock when predicting the apparent influence of SST on run timing.

Conclusions

1) Sea surface temperature in the Gulf of Alaska is significantly statistically related to adult run timing in seven Fraser and six non-Fraser Gulf of Alaska sockeye stocks or stock-groupings.
2) These relationships are largely consistent with the postulations of a simple temperature-displacement model.
3) Relevant sea surface temperature data are available in time for preseason predictions of approximate adult run timing to be made for many stocks of all species of Pacific salmon.

Acknowledgements

This type of analysis would not have been possible without the data provided by the efforts of almost all the staff since the inception of the Commission. I am particularly indebted to all my colleagues, past and present, in the Management and Operations Divisions. I am also very grateful to several people in Alaska, British Columbia, and Washington who provided me with advice and unpublished run timing data. I thank Vic Aro of the Canada Department of Fisheries and Oceans and Colin Harris of the Fisheries Research Institute, University of Washington for tagging data on Fraser and Chignik sockeye. Dr. D. McLain (N.M.F.S., Monterey) kindly provided me with essential unpublished sea surface temperature data.

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Application of Scale Patterns Analysis to the Management of Alaska's Sockeye Salmon (*Oncorhynchus nerka*) Fisheries

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Abstract

Marshall, S., D. Bernard, R. Conrad, B. Cross, D. McBride, A. McGregor, S. McPherson, G. Oliver, S. Sharr, and B. Van Alen. 1987. Application of scale patterns analysis to the management of Alaska's sockeye salmon (*Oncorhynchus nerka*) fisheries, p. 307–326. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The biological aspect of sockeye salmon (*Oncorhynchus nerka*) management centers around a relatively simple rule: regulate the harvest so that an escapement goal is met. While the rule is simple, implementation is not. Production units (stocks) need to be identified, escapement goals determined, and inseason management procedures developed to achieve concurrent biological and social management objectives. Further, the mixed stock nature of most sockeye salmon fisheries adds complexity to the task. From examples drawn throughout Alaska, we illustrate how scale patterns analysis is contributing to an integrated fishery management program.

Résumé

Marshall, S., D. Bernard, R. Conrad, B. Cross, D. McBride, A. McGregor, S. McPherson, G. Oliver, S. Sharr, and B. Van Alen. 1987. Application of scale patterns analysis to the management of Alaska's sockeye slamon (*Oncorhynchus nerka*) fisheries, p. 307–326. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

L'aspect biologique de la gestion du saumon nerka (*Oncorhynchus nerka*) est axée sur une règle relativement simple : réglementer l'exploitation afin de fixer l'échappée. Quoique cette règle soit simple, sa mise en vigueur ne l'est pas. Il est nécessaire d'identifier les unités de production (stocks), de fixer l'échappée et de mettre au point des procédures de gestion saisonnière afin d'atteindre les objectifs biologiques et sociaux en matière de gestion. De plus, étant donné que la plupart des ressources de saumon nerka sont composées de stocks mixtes, la complexité de la tâche est amplifiée. À partir d'exemples relevés en Alaska, les auteurs montrent comment l'analyse des écailles contribue à un programme intégré de gestion de la pêche.

Introduction

Management of Pacific salmon (*Oncorhynchus* sp.) fisheries is an active process of conservation and allocation of fisheries resources. Management objectives are established to fulfill the economic, social, and legal demands of the public within the biological constraints of the resource. The dual responsibility of the fisheries manager to conserve and to allocate has been the impetus for development and implementation of new techniques of stock assessment, such as stock identification by scale patterns analysis (SPA).

Scale patterns analysis is a tool to estimate stock-specific catch in mixed-stock fisheries. Such estimates are used to set annual escapement goals, to meet these annual goals through regulation of catch during a fishery, and to document entitlements and thereby allocate fisheries resources.

In this paper are five examples of how SPA has been used to conserve and allocate resources in several of Alaska's fisheries for sockeye salmon (*O. nerka*) (Fig. 1). First, the catches of five runs through seven separate fisheries in upper Cook Inlet are estimated with SPA to expose opportunities for more stock-specific, in-season management. Second, SPA is used to discover the importance of stocks other than those of the Copper River to local fisheries. Third, SPA is shown to improve efficacy of in-season decisions to change management emphasis between two runs in the Chignik fishery. Fourth, stratifying catch-per-unit-of-effort (CPUE) statistics from the Lynn Canal fishery by stock, using SPA, is shown to significantly reduce the variation of inputs to models used for in-season forecasting of run strength. Finally, SPA on catches from stocks returning to transboundary rivers illustrates how concurrent objectives of conservation and allocation can be met in a single, integrated program.

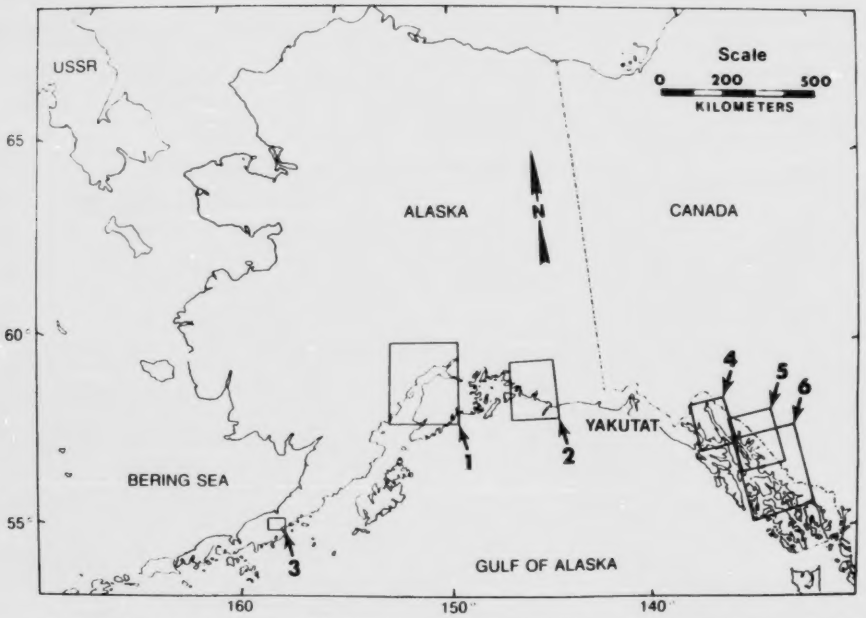

FIG. 1. Location of study areas in Alaska and western Canada: (1) Cook Inlet, (2) Copper–Bering Rivers, (3) Chignik, (4) Lynn Canal, (5) Taku–Snettisham, and (6) Sumner Straits–Stikine.

What Is Scale Patterns Analysis?

Scale patterns analysis is based on differences in the arrangement of circuli on scales. These patterns are histories of growth. Salmon with similar histories have similar scale patterns, while those with different histories exhibit different patterns. The greater the difference among scale patterns, the better one pattern can be distinguished from another. The first step in an SPA is to collect scales from escapements (or other source of known origin) and from catches. Several aspects of these scales are measured, thereby building data sets of variables that describe the typical pattern for each stock or group of stocks. Next, the data sets from the escapements are compared against each other using statistical techniques to build a decision rule which can be used to classify scales as belonging to one of the groups. The accuracy of the decision rule is tested with fish of known origin to estimate coefficients of misclassification for a linear correction matrix. Finally, the decision rule and its correction matrix are used to classify fish of unknown origin from a mixture (the catches) into one of the groups.

The precision of estimates from SPA is dependent upon (a) the accuracy of the uncorrected decision rule, (b) the size of the sample used to construct and evaluate the rule, (c) the size of the sample drawn from the mixed stocks (Pella and Robertson 1979), and (d) the precision of the estimated contribution for each age when the analysis is stratified by age group (Oliver et al. 1985). Many methods of building decision rules have been developed, including linear discriminant functions (Fisher 1936), quadratic discriminant functions (Smith 1947), polynomial discriminant functions (Specht 1966) and nearest neighbor analysis (Clover and Hart 1967). A leaving-one-out (jackknife) procedure (Lachenbruch 1967) has proven to be the most efficient method of estimating misclassification error by a decision rule, and the linear correction matrix of Cook and Lord (1978) has proven to be the most effective means to correct these errors.

For an SPA, stocks of Pacific salmon have been pooled (grouped) into convenient sets based on the needs of management and differences in scale patterns. Scale patterns analysis has been used to differentiate among stocks within a river (Henry 1961; Marshall et al. 1980; McBride and Marshall 1982), among rivers within common fisheries (Cook and Lord 1978; McGregor and Marshall 1982; Van Alen 1982; Conrad 1984a), and among large geographic regions, nations, or continents for salmon caught in a common fishery (Anas and Murai 1969; Bilton and Messinger 1975; Marshall et al. 1978; Cook 1982; Marshall et al. 1984; Rogers et al. 1984; and Oliver et al. 1985). Regardless of the grouping of stocks, all pooled groups in the catch must be represented in the decision rule because each fish will be assigned to one of the groups whether that fish is a member of the groups in the SPA or not.

Upper Cook Inlet

OVERVIEW

The drift and set gillnet fisheries of upper Cook Inlet (Fig. 2) harvested an average 2.1 million sockeye salmon annually from 1975 to 1984. Tagging studies (Thompson 1930; Noerenberg and Calkins 1959) demonstrate that these fisheries exploit stocks originating in local rivers, mainly the Kenai, Kasilof, Susitna, and Crescent rivers and Fish Creek. Two, 12-h fishing periods are usually permitted each week with more or fewer periods depending on run size. Until recently, the weekly schedule has been adjusted only slightly. Hydroacoustic technology is used to count escapements

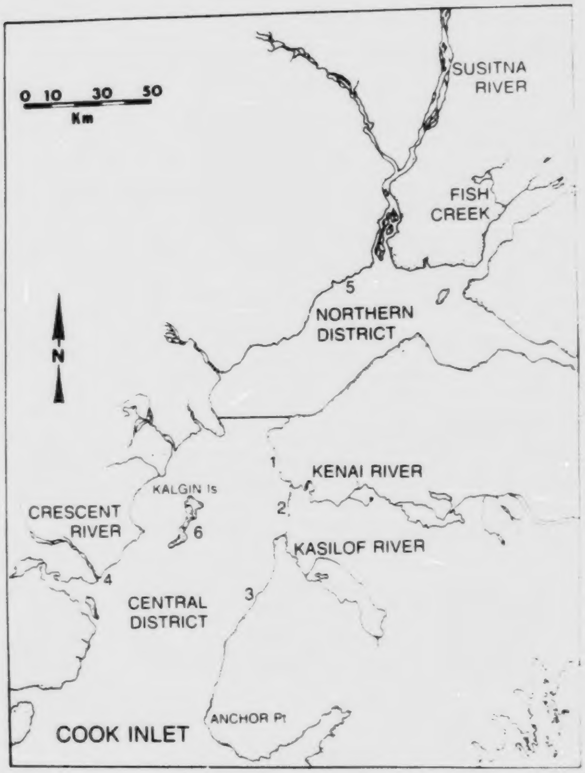

FIG. 2. The upper Cook Inlet area showing the location of the fisheries and major drainages supporting sockeye salmon. Setnet fisheries are (1) Salamatof Beach, (2) Kalifonski Beach, (3) Cohoe/Ninilchik Beach, (4) West-side, (5) Northern, and (6) Kalgin. The driftnet fishery operates in the Central District.

into the visually occluded rivers of the region (Namtvedt et al. 1978). Escapement goals were established as this technology was developed and as statistics on catches and escapements were compiled for each river (Cross et al. 1983a). Age-group 1.3 has dominated the returns to the Inlet in recent years (90% in 1978, 59% in 1979, 49% in 1980, 74% in 1981, and 89% in 1982).

Since 1978, contributions by river of origin to the harvests of sockeye salmon in upper Cook Inlet have been estimated (Bethe et al. 1980; Cross et al. 1981, 1982, 1983b, 1985). Davis (1972) attempted to estimate catches of two stocks from Kenai River in set nets along the beaches of the eastern side of the Central District. Later, Bethe and Krasnowski (1979) found that SPA can be used to differentiate runs of sockeye salmon returning to the Kenai, Kasilof, and Susitna rivers. Today, SPA is used during the fishery to estimate catches of sockeye salmon returning to the major rivers.

THE RIVER STOCKS.

The Kenai River has been the largest producer of sockeye salmon in upper Cook Inlet, and from 1978 to 1982 represented from 36 to 67% of the total return (Table 1). This run has comprised a significant portion of the catch in all fisheries, except for the westside set net fishery (Table 2). The drift gillnet fishery has subjected these fish to exploitation rates from 0.24 (1979) to 0.64 (1978). The eastside set net fisheries as a whole exploited these fish at rates from 0.15 (1978) to 0.27 (1982).

The Kasilof River has been the second largest producer of sockeye salmon in the Inlet with 18 to 31% of the total return from 1978 to 1982 (Table 1). The drift gillnet and eastside set net fisheries equally exploit this run with average rates of 0.38 and 0.32, respectively (Table 2). Over the past

TABLE 1. Catch and escapement by river for upper Cook Inlet, 1978–82.[a]

River		1978	1979	1980	1981	1982
Kenai	Catch	1 817 558	314 424	527 848	585 719	1 718 537
	Escapement	407 977	289 579	470 914	412 909	631 537
	Return	2 225 535	604 003	998 762	998 628	2 350 074
	% Inlet Return	67.1	36.0	38.8	39.1	53.0
Kasilof	Catch	479 136	299 505	600 491	331 858	1 066 816
	Escapement	116 600	152 179	187 154	267 368	190 235
	Return	595 736	451 684	787 645	599 226	1 257 051
	% Inlet Return	18.0	26.9	30.6	23.5	28.3
Susitna	Catch	284 539	219 804	324 064	423 865	277 761
	Escapement	94 400	156 890	190 866	340 232	265 332
	Return	378 939	376 694	514 930	764 097	543 093
	% Inlet Return	11.4	22.4	20.0	29.9	12.2
Crescent	Catch	34 914	41 480	71 970	19 719	145 941
	Escapement	74 000	86 654	90 863	41 213	58 957
	Return	108 914	128 134	162 833	60 932	204 898
	% Inlet Return	3.3	7.6	6.3	2.4	4.6
Fish	Catch	5 520	49 193	49 255	78 059	50 809
	Escapement	3 555	68 739	62 628	50 479	28 164
	Return	9 075	117 932	111 883	128 538	78 973
	% Inlet Return	0.3	7.0	4.3	5.0	1.8
Total	Catch	2 621 667	924 406	1 573 628	1 439 220	3 259 864
	Escapement	696 532	754 041	1 002 425	1 112 201	1 174 225
	Return	3 318 199	1 678 447	2 576 053	2 551 421	4 434 089

[a] Errors were found in statistics reported by Bethe et al. (1980) and Cross et al. (1982) and were corrected for this analysis.

TABLE 2. Catch and exploitation rates by river and fishery for upper Cook Inlet, 1978–82.

			Eastside set net fishery						
River	Year	Drift	Cohoe/ Ninilchik	Kalifonsky	Salamatof	West-Side	Kalgin	Northern	Total
Kenai River									
Number caught	1978	1 432 193	109 746	95 962	143 040	3 734	27 680	5 203	1 817 558
	1979	145 964	28 686	23 315	36 732	5 379	9 143	65 205	314 424
	1980	278 275	68 026	45 726	78 368	5 796	11 670	39 987	527 848
	1981	251 640	94 027	54 760	117 291	2 073	9 403	56 525	585 719
	1982	1 055 287	129 487	150 159	358 111	—[a]	6 427	19 066	1 718 537
Percent contribution to catch	1978	79.4	50.8	54.9	53.0	5.9	65.5	10.1	69.3
	1979	32.1	23.8	49.0	45.4	8.5	20.3	58.0	34.0
	1980	36.1	22.9	36.8	59.7	7.2	20.4	37.9	33.5
	1981	39.8	36.6	54.4	84.7	7.8	27.7	22.6	40.7
	1982	50.2	40.5	58.5	90.7	—[a]	16.2	16.1	52.7
Exploitation rate	1978	0.64	0.05	0.04	0.06	0.01	0.01	0.01	0.82
	1979	0.24	0.05	0.04	0.06	0.01	0.01	0.11	0.52
	1980	0.28	0.07	0.04	0.08	0.01	0.01	0.04	0.53
	1981	0.25	0.09	0.05	0.12	0.01	0.01	0.06	0.59
	1982	0.45	0.06	0.06	0.15	—[a]	—[b]	0.01	0.73
Kasilof River									
Number caught	1978	211 182	78 867	65 413	95 372	12 468	5 546	10 288	479 136
	1979	155 418	78 887	20 652	25 483	2 459	16 606	—[a]	299 505
	1980	243 640	199 503	70 254	52 372	3 270	31 452	—[a]	600 491
	1981	155 910	124 527	30 312	8 334	1 511	11 264	—[a]	331 858
	1982	773 140	186 319	83 040	—[a]	—[a]	24 317	—[a]	1 066 816
Percent contribution to catch	1978	11.7	36.5	37.5	35.3	19.6	13.1	19.9	18.3
	1979	34.1	65.6	43.4	31.5	3.8	36.9	—[a]	32.4
	1980	31.6	65.6	56.7	39.9	4.0	54.9	—[a]	38.2
	1981	24.6	48.4	30.1	6.0	5.8	33.2	—[a]	23.1
	1982	36.7	58.3	32.4	—[a]	—[a]	61.3	—[a]	32.7
Exploitation rate	1978	0.35	0.13	0.11	0.16	0.02	0.01	0.02	0.80
	1979	0.34	0.17	0.05	0.06	—[b]	0.04	—[a]	0.66
	1980	0.31	0.25	0.09	0.07	—[b]	0.04	—[a]	0.76
	1981	0.26	0.21	0.05	0.01	—[b]	0.02	—[a]	0.55
	1982	0.62	0.15	0.07	—[a]	—[a]	0.02	—[a]	0.85
Susitna River									
Number caught	1978	157 063	26 875	12 772	30 709	19 937	3 754	33 429	284 539
	1979	118 410	12 713	3 267	18 705	15 266	18 089	33 354	219 804
	1980	214 030	31 595	8 127	0	7 890	8 110	54 312	324 064
	1981	197 097	36 710	14 493	11 469	4 613	8 846	150 637	423 865
	1982	117 665	—[a]	23 220	35 291	10 527	7 367	83 691	277 761
Percent contribution to catch	1978	8.7	12.4	7.3	11.4	31.4	8.9	64.8	10.9
	1979	26.1	10.6	6.8	23.1	24.1	40.2	29.7	23.8
	1980	27.8	9.7	6.5	0.0	9.8	14.1	51.4	20.6
	1981	31.1	14.3	14.4	8.3	17.6	26.1	60.4	29.4
	1982	5.6	—[a]	9.0	8.9	38.5	18.6	70.9	8.5
Exploitation rate	1978	0.42	0.07	0.03	0.08	0.05	0.01	0.09	0.75
	1979	0.31	0.03	0.01	0.05	0.04	0.05	0.09	0.58
	1980	0.42	0.06	0.02	0.00	0.02	0.02	0.11	0.63
	1981	0.26	0.05	0.02	0.01	—[b]	0.01	0.20	0.55
	1982	0.22	—[a]	0.04	0.07	0.02	0.01	0.15	0.51
Crescent River									
Number caught	1978	—[a]	—[a]	—[a]	—[a]	27 373	5 204	2 337	34 914
	1979	—[a]	—[a]	—[a]	—[a]	40 338	1 142	0	41 480
	1980	—[a]	—[a]	—[a]	—[a]	63 672	6 062	2 236	71 970
	1981	0	—[a]	—[a]	—[a]	18 075	1 644	0	19 719
	1982	123 931	—[a]	—[a]	—[a]	16 547	496	4 967	145 941
Percent contribution to catch	1978	—[a]	—[a]	—[a]	—[a]	43.1	12.3	4.5	1.3
	1979	—[a]	—[a]	—[a]	—[a]	63.6	2.6	0	4.5
	1980	—[a]	—[a]	—[a]	—[a]	79.0	10.6	2.1	4.6

TABLE 2. (*Continued.*)

			Eastside set net fishery						
River	Year	Drift	Cohoe/ Ninilchik	Kalifonsky	Salamatof	West-Side	Kalgin	Northern	Total
	1981	0.0	—[a]	—[a]	—[a]	68.8	4.8	0	1.4
	1982	5.9	—[a]	—[a]	—[a]	60.6	1.3	4.2	4.5
Exploitation rate	1978	—[a]	—[a]	—[a]	—[a]	0.25	0.05	0.02	0.32
	1979	—[a]	—[a]	—[a]	—[a]	0.31	0.01	0.00	0.32
	1980	—[a]	—[a]	—[a]	—[a]	0.39	0.04	0.01	0.44
	1981	0.00	—[a]	—[a]	—[a]	0.29	0.03	0.00	0.32
	1982	0.60	—[a]	—[a]	—[a]	0.08	—[b]	0.03	0.71
Fish Creek									
Number caught	1978	3 041	724	504	813	—[a]	71	367	5 520
	1979	34 915	0	388	0	—[a]	0	13 890	49 193
	1980	34 302	5 278	82	481	—[a]	0	9 112	49 255
	1981	28 498	1 852	1 087	1 334	—[a]	2 788	42 500	78 059
	1982	33 406	4 022	239	1 535	233	1 038	10 336	50 809
Percent contribution to catch	1978	0.2	0.3	0.3	0.3	—[a]	0.2	0.7	0.2
	1979	7.7	0.0	0.8	0.0	—[a]	0.0	12.3	5.3
	1980	4.5	1.8	—[b]	0.4	—[a]	0.0	8.6	3.1
	1981	4.5	0.7	1.1	1.0	—[a]	8.2	17.0	5.4
	1982	1.6	1.2	0.1	0.4	0.9	2.6	8.8	1.6
Exploitation rate	1978	0.33	0.08	0.06	0.09	—[a]	0.01	0.04	0.61
	1979	0.30	0.00	—[b]	0.00	—[a]	0.00	0.12	0.42
	1980	0.31	0.05	—[b]	—[b]	—[a]	0.00	0.08	0.44
	1981	0.22	0.02	0.01	0.01	—[a]	0.02	0.33	0.61
	1982	0.42	0.05	—[b]	0.02	—[b]	0.02	0.13	0.64

[a] Stock not included in classification model.

[b] Exploitation rate is less than 0.01.

6 years, these exploitation rates have been too low to harvest the surplus production of this artificially enhanced run.

The stocks of the Susitna River have ranked third, averaging 19.2% of the total return to upper Cook Inlet from 1978 to 1982 (Table 1). The drift gillnet fishery in the Central District and the set net fishery in the Northern District are the major harvesters of this run with average annual exploitation rates of 0.33 and 0.12, respectively (Table 2). Sockeye salmon bound for the Susitna River can be found in all the fishing districts in upper Cook Inlet.

The much smaller runs to Crescent River and Fish Creek respectively represent only 4.8 and 3.5% of the return to the Inlet from 1978 to 1982 (Table 1). The indicated small contribution from the Crescent River is due in part to exclusion of this river from SPA for many fishing districts (Table 2).

In contrast, Fish Creek has been included in the SPA for almost all fisheries in the Inlet, yet was found to have contributed little to catches. The drift gillnet fishery in the Central District and set net fishery in the Northern District have had the greatest impact on the run to Fish Creek with average exploitation rates of 0.32 and 0.14, respectively.

SPA AND MANAGEMENT.

Besides a postseason tally of catches by district and run, SPA can be used to reveal migratory patterns that can aid managers in targeting fishing effort on specific runs. Comparison among runs of CPUE statistics across fishing district can expose times and areas when one run can be harvested without significant harvest of another. In this comparison across upper Cook Inlet, boat-hour (drift gillnet) and permit-hour (set net) are the units of effort and fish aged 1.3 is the unit of catch. Because SPA was conducted only for fish of age 1.3 in 1978–82, use of this age-group provides the most direct comparison.

There is some opportunity to direct fishing effort to specific stocks in the drift fishery in the Central District. Inspection of CPUE by fishing period shows that in most years the bulk of the run to the Kasilof River enters the district before the other two runs (Fig. 3). The mean dates of migration (see Mundy 1982) for 1978–82 are 6 July for the Kasilof River, 9 July for the Susitna River, and 14 July for the Kenai River (Table 3). After 6 July, the bulk of the fish bound for both the Kenai and Susitna rivers enter the district (Table 3.) The timing of the migration to the Susitna River has been more condensed than that to the Kenai River (Fig. 3) with negligible CPUE after 20 July. Therefore in most years fish that are present in the Central District after 20 July are migrating to the Kenai River (Fig. 4).

Opportunity to selectively exploit some stocks through differences in migratory timing extends to the set net fishery on the eastside of the Central District. Mean dates of CPUE on Cohoe/Ninilchik, Kalifonsky, and Salamatof beaches show that fish bound for the Kasilof River enter the fishery first, fish bound for the Susitna River next, and fish for the Kenai River last (Table 3). Also, fish from all rivers tend to be present on the southern beaches earlier and the northern beaches later (Table 3). On the two southern beaches, Cohoe/Ninilchik and Kalifonsky, the fraction of the catch bound for the Kenai River builds as July progresses (Fig. 5 and 6) while the fraction of fish bound for the Kasilof River subsides.

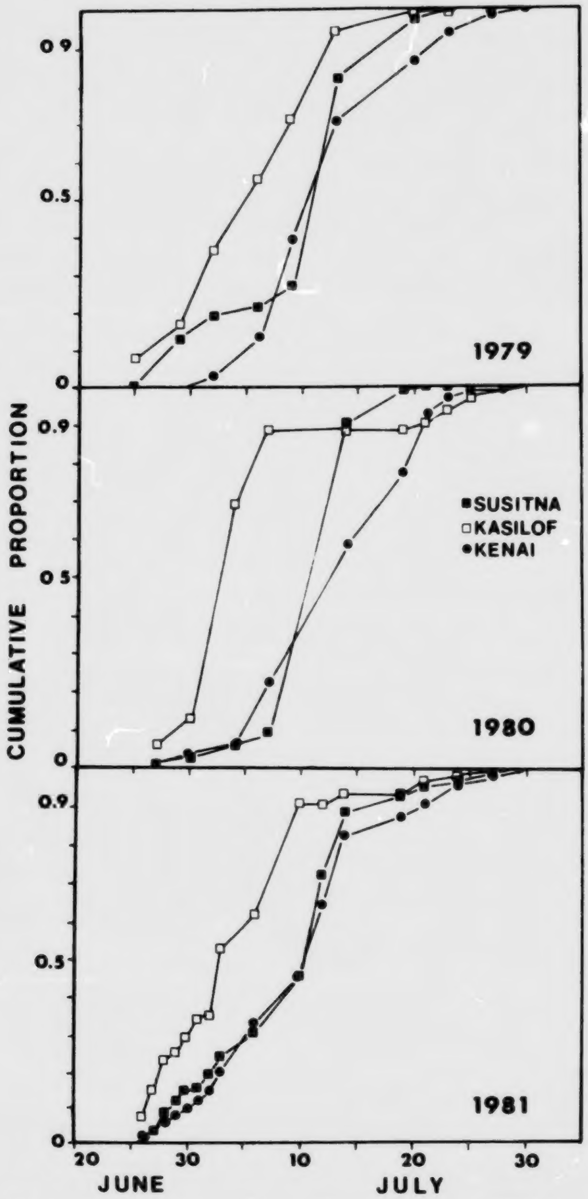

FIG. 3. Cumulative proportion of catch-per-unit-of-effort (see Mundy 1982) in the drift fishery of age 1.3 sockeye salmon bound for the Kenai, Kasilof, and Susitna rivers 1979–81. Boat-days is the unit of effort.

Scale patterns analysis has also been used to reveal some opportunities for effective use of area openings and closures of the eastside set net fishery. For 1978–82, the average exploitation rates on fish from the Kenai River has been lowest on Kalifonsky Beach (4.6%) and highest on Salamatof Beach (9.4%) with the rate intermediate on Cohoe/Ninilchik/Beach (6.4%) (from Table 2). Since the three beaches have usually been opened or closed as a unit, the low exploitation rate on Kalifonsky Beach could be partially the result of catches made on Cohoe/Ninilchik.

In contrast, the average exploitation rates on fish bound for the Kasilof River for the same years is higher on Cohoe/Ninilchik Beach (18.2%) and lower on Salamatof and Kalifonsky beaches (7.5 and 7.4%, respectively) (from Table 2).

If there are no opportunities for stock-specific harvest in existing fishing areas, new areas may be created. Scale patterns analysis has revealed that in Cook Inlet, fish bound for Fish Creek are exploited in the Central and Northern Districts (from Table 2, 54.4% on average from 1978 to 1982). But even with this high rate of exploitation, escapements have exceeded the goal of 50 000 (118 797 in 1983 and 192 352 in 1984). Scale patterns analysis of catches from different subdistricts has revealed no opportunity to selectively exploit this stock. Because catches of these fish are miniscule relative to those of other runs (Table 2), management of existing fisheries to increase the catch of this enhanced stock is not desirable. Therefore, in 1985, the Alaska Board of Fisheries, responding to these circumstances, created a new set net fishery adjacent to the mouth of Fish Creek.

Use of SPA in upper Cook Inlet is being expanded and adapted to the ever quickening pace of management. Along with the 1.3 age-group, catches of other major age-groups, such as age 1.2 are now being partitioned directly into the river of origin using SPA. An in-season program based on SPA currently provides estimates of catches by river of origin after each fishing period and before the following one to augment historical data on migratory timing, and the efficacy of many new restrictions in fishing boundaries is being tested with SPA. New ways of using SPA will continue to improve the precision of the fisheries management in upper Cook Inlet.

The Copper–Bering River Fisheries

OVERVIEW

Drift gillnet fisheries offshore of the Copper (District 212) and Bering rivers (District 200) (Fig. 7) harvested on average

TABLE 3. Mean date of migration through selected fisheries as computed from catch-per-unit-effort statistics of age 1.3 sockeye salmon, 1978–82. Boat-days for the drift fishery and permit-hours for the set net fishery are the units of effort. (ND = No data).

			Eastside set net fisheries		
Stock	Year	Drift fishery	Cohoe/ Ninilchick	Kalifonsky	Salamatof
Kenai River	1978	14 July	16 July	16 July	18 July
	1979	13 July	19 July	17 July	17 July
	1980	14 July	17 July	18 July	21 July
	1981	10 July	10 July	14 July	14 July
	1982	19 July	21 July	22 July	22 July
	x̄, SE	14.0, 1.3	16.0, 1.7	17.4 1.9	18.4, 1.3

TABLE 3. (*Continued.*)

			Eastside set net fisheries		
Stock	Year	Drift fishery	Cohoe/ Ninilchick	Kalifonsky	Salamatof
Kasilof River	1978	8 July	12 July	16 July	16 July
	1979	6 July	2 July	4 July	10 July
	1980	6 July	11 July	15 July	20 July
	1981	5 July	2 July	30 June	8 July
	1982	ND	ND	ND	ND
	$\bar{x}$, SE	6.3, 0.5	6.8, 2.4	8.8, 3.5	13.5, 2.4
Susitna River	1978	2 July	18 July	19 July	16 July
	1979	11 July	5 July	6 July	16 July
	1980	13 July	8 July	9 July	No Catch
	1981	9 July	10 July	15 July	14 July
	1982	ND	ND	ND	ND
	$\bar{x}$, SE	8.8, 2.1	10.3, 2.4	12.3, 2.5	15.3, 0.5
Susitna/Kasilof Rivers combined	1982	14 July	13 July	18 July	19 July

approximately 605 000 sockeye salmon annually during 1975–84 (Sharr et al. 1985a). Catches were presumed to be from stocks that migrate through the Copper River to spawning grounds in interior Alaska (Upriver stocks) and from stocks that spawn in streams in the Copper River Delta or around the Bering River (Delta stocks) (Thompson 1964). The Upriver stocks were presumed to be the only significant source of production for this fishery (Pirtle 1967) and in 1978, hydroacoustic counters were installed at Miles Lake (Fig. 7) to estimate their escapements. Later, Mundy et al. (1984) proposed using historic statistics on CPUE in the fishery along with migratory timing past the site at Miles Lake to estimate abundance of sockeye salmon in the fishing districts during a fishery. From this paradigm, the fishery has been regulated primarily to attain an escapement past the counting site at Miles Lake. Aerial surveys of streams of the Copper River Delta and the area around the Bering River have been used to estimate an index of escapement to these areas.

DELTA STOCKS

The importance of Delta stocks to the local fishery was demonstrated with SPA (Sharr 1983a; Sharr et al. 1984; Sharr and Goshert 1985a, 1985b). A list of differences between Upriver and Delta stocks includes migratory timing, age of maturity, and lacustrine growth as recorded on scales (Thompson 1964) and age composition (Larson and Fridgen 1968; Sharr 1983b; Sharr et al. 1985).

First Pirtle (1967) and then Roberson and Fridgen (1972) suggested that scale patterns might be useful in differentiating catches of Delta and Upriver stocks. Since 1982, those aspects of scale patterns that relate to lacustrine and early marine growth have been used to estimate catches from Upriver and Delta stocks. During the years 1982–84, Delta stocks contributed 49%, 48% and 21%, respectively, of the catches in the Copper–Bering River fisheries.

The unexpectedly large numerical and economic contributions of sockeye salmon from the Delta stocks has prompted a broadened management emphasis. Currently, the annual catch and escapement statistics for the Delta stocks are too few for estimating an escapement that will optimize production, and SPA of catches from various subdistricts shows that stocks are thoroughly mixed in this fishery (Sharr 1983a) (Fig. 8–10). However, a new in-season program of SPA provides weekly estimates of catch by age and catch by run that will permit at least minimum protection of the production from the Delta stocks.

INTERCEPTIONS

Soon after its opening in 1978 the Kayak Island fishery in subdistrict 200–30 south of Kayak Island (Fig. 7) was producing a catch in excess of that from more traditional sub districts 200–10 and 200–20 (Fig 11). In 1983 a proposal to close the Kayak Island fishery was made to the Alaska Board of Fisheries which has a policy of limiting unnecessary new interception fisheries (Alaska Department of Fish and Game 1985). Acceptance of the proposal would depend upon proof that the fishery in question intercepted significant numbers of sockeye salmon bound elsewhere.

Proof was provided at minimal cost through SPA (McBride et al. 1984). A decision rule was derived from scales collected in 1982 to distinguish catches from Upriver stocks, some Delta stocks, and a stock from the area around Yakutat, Alaska (Fig. 1) The Yakutat stock was included in the decision rule because (1) Yakutat is near Kayak Island, (2) Yakutat stock productivity had been unusually poor, (3) Yakutat age composition had been similar to that of fish caught in the Kayak Island fishery, and (4) fish arrive at the Yakutat area soon after most of the Kayak Island fishery was concluded. Some stocks from the area around the Bering River were excluded because they reached their natal streams before the bulk of the catches were made in the Kayak Island fishery.

When the decision rule was applied to scales collected from the Kayak Island fishery in 1982, 6% and 41% were estimated to be from other than local stocks in mid-June and mid-July, respectively. These estimates do not necessarily demonstrate interception of the Yakutat stock, but rather interception of stocks with growth histories and scale patterns atypical of the local Delta and Upriver stocks. Although catches cannot be allocated with SPA on this basis, these results are sufficient to conclude that the Kayak Island fishery was

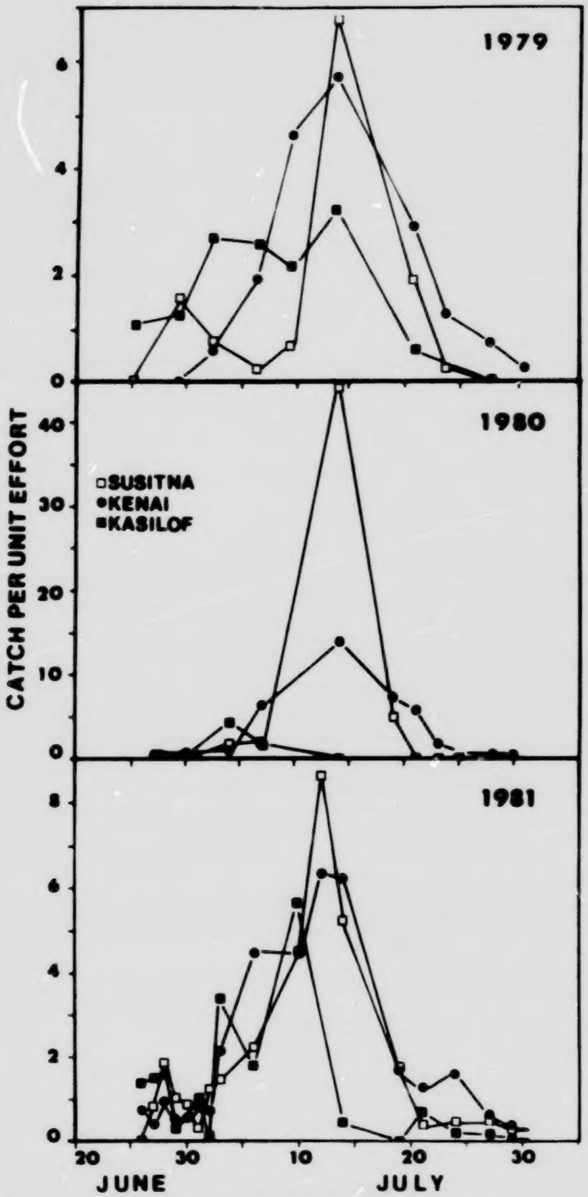

FIG. 4. Catch-per-unit-of-effort in the drift fishery of age 1.3 sockeye salmon bound for the Kenai, Kasilof, and Susitna rivers 1979 to 1981. Boat-days is the unit of effort.

an interception fishery in 1982. This conclusion was verified in 1985 when 110 sockeye salmon were tagged in subdistrict 200-30 and later recovered in Prince William Sound (54), the traditional fishing areas of District 200 and 212 (40), Cook Inlet (14), and Yakutat (2) McCurdy (1985). In 1986, the Alaska Board of Fisheries closed the Kayak Island fishery.

The Chignik Fishery

OVERVIEW

The Chignik watershed (Fig. 12) consists of Black and Chignik lakes, their tributaries and a lower river emptying into a saltwater lagoon. The local purse seine fishery has harvested an average of 1.49 million sockeye salmon annually (1975-84) from the two major runs to this watershed. The early run usually arrives in June, spawns in the tributaries of Black Lake, and progeny typically smolt after a single year's residence in this lake; the late run usually arrives in July, spawns in the tributaries and along the beaches of Chignik Lake, and its progeny typically smolt after two years in this lake (Burgner and Marshall 1974). Because inter- and intraspecific competition in the two nursery lakes limits production of sockeye salmon from the watershed (Narver 1966), escapement goals were established for each major run to optimize fry production. Until 1981, the switch in management emphasis from the early to late runs (i.e. change in fishing time) occurred on a date picked from an average time-of-entry (TOE) curve when each run comprised about half the fish in the fishery.

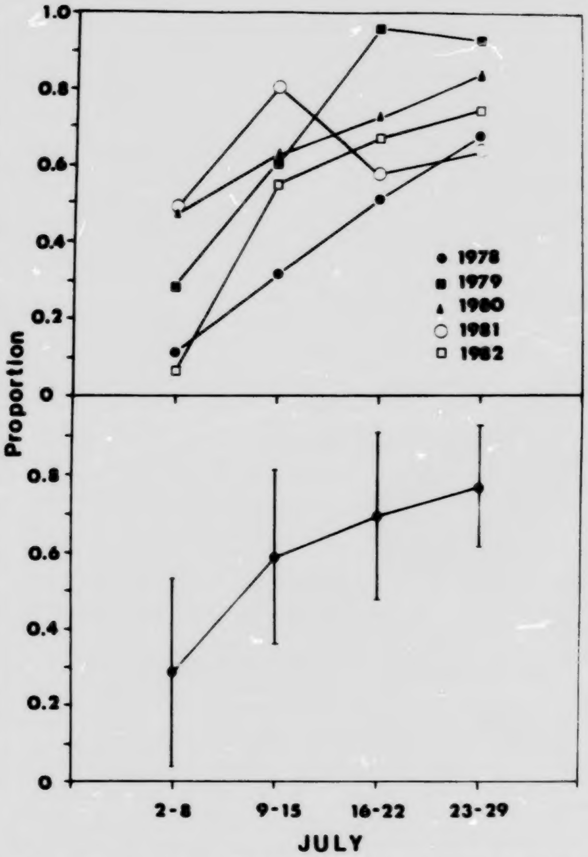

FIG. 5. Temporal pattern of the contribution of Kenai River age 1.3 sockeye salmon in weekly catches on Kalifonsky Beach. Upper frame presents weekly proportions by year and the lower frame presents the 1978-1982 mean and 95% confidence intervals.

TIME-OF-ENTRY CURVES

From data obtained through mark recapture experiments, Dahlberg (1968) developed a method of estimating the daily catch and escapement for the early and late runs of adult sockeye salmon to the watershed. From 1962 to 1966, adults were tagged annually at a weir below Chignik Lake with variously colored Petersen disks to signify the date(s) of tag-

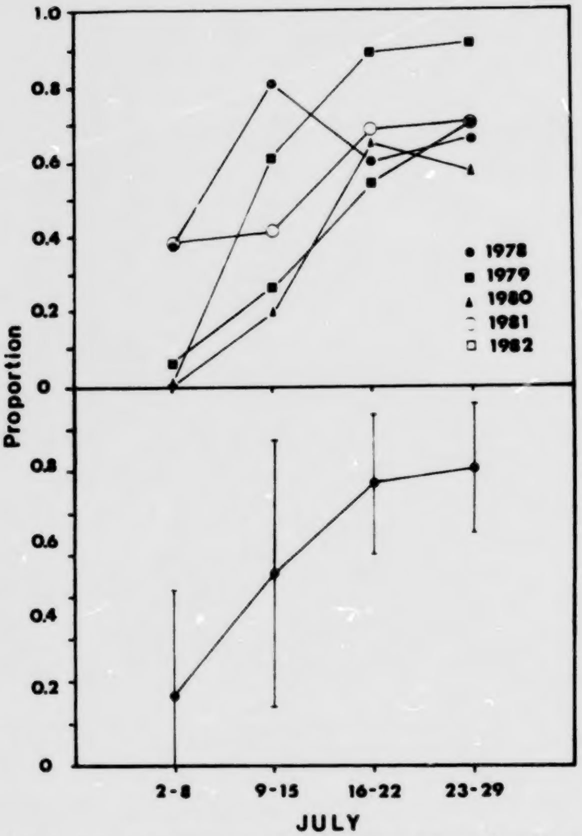

FIG. 6. Temporal pattern of the contribution of Kenai River age 1.3 sockeye salmon in weekly catches on Cohoe/Ninilchik Beach. Upper frame presents weekly proportions by year and the lower frame presents the 1978–82 mean and 95% confidence intervals.

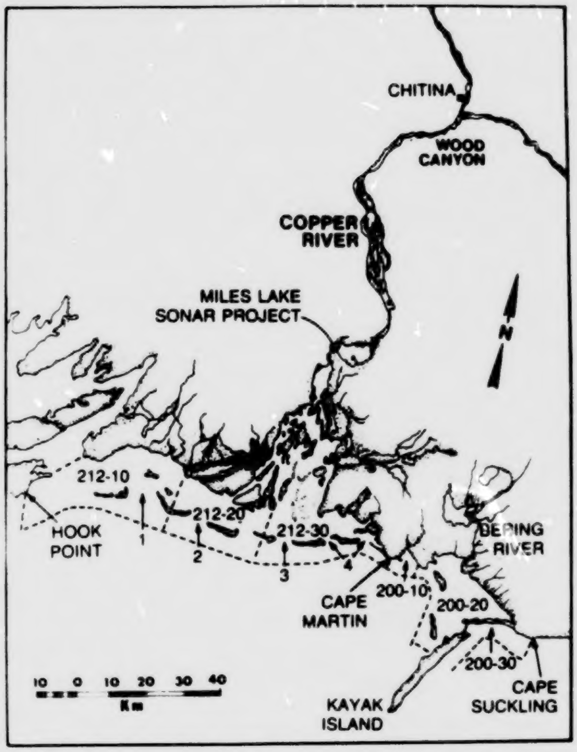
CHITINA
WOOD CANYON
COPPER RIVER
MILES LAKE SONAR PROJECT
N
212-10
212-20
212-30
HOOK POINT
1
2
3
4
BERING RIVER
200-10
200-20
200-30
CAPE MARTIN
CAPE SUCKLING
KAYAK ISLAND
10 0 10 20 30 40
Km

FIG. 7. The Copper–Bering rivers area showing the location of the fisheries and major sockeye salmon spawning drainages. Channels of the Copper River Delta fishing district (212-10 through 212-30) and (1) Egg Island, (2) Pete Dahl, (3) Kokinhenik, and (4) Softuk. The Bering River fishing district is numbered 200-10 through 200-30.

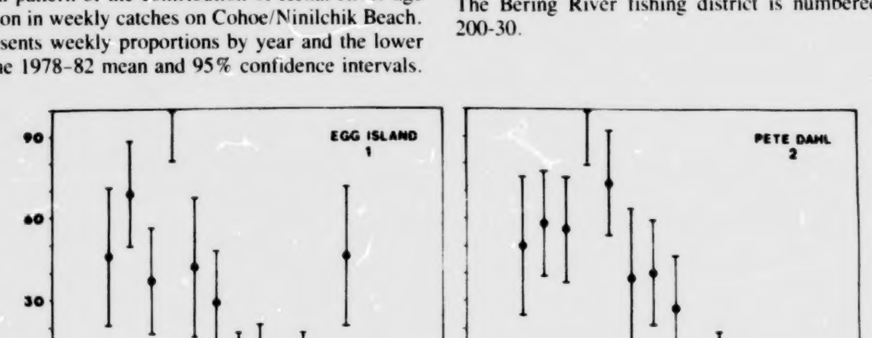

FIG. 8. Percent contributions of the Upriver stock to weekly catches of age 1.3 sockeye salmon in four channels of the Copper River district in 1982. (See fig. 7 for location of channels.)

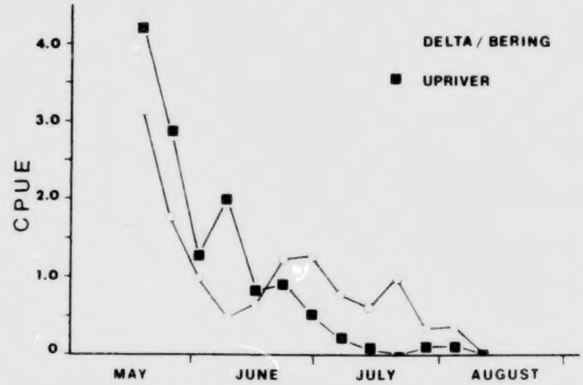

FIG. 9. Catch-per-unit-of-effort of Upriver and Delta origin of salmon aged 1.3 in the Copper River district fishery during 1982. Boat-days is the unit of effort.

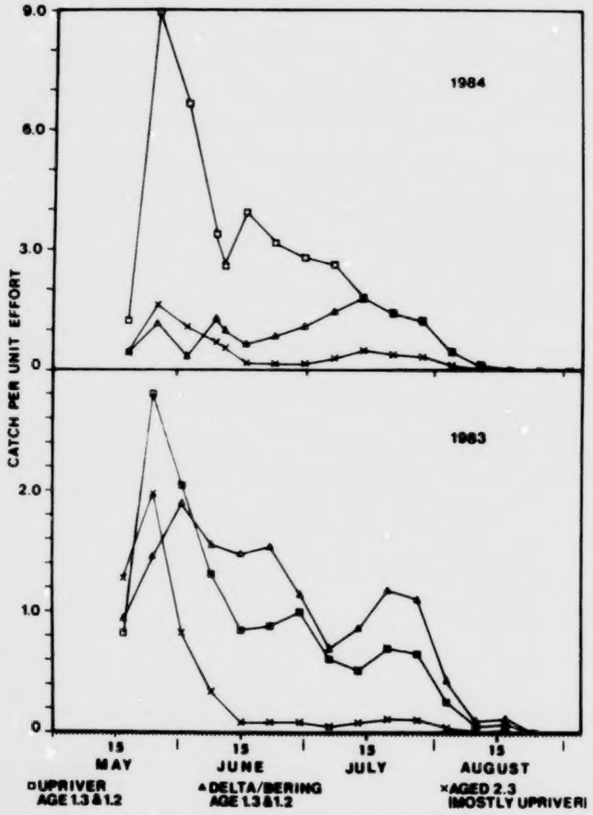

FIG. 10. Catch-per-unit-of-effort of Upriver and Delta fish aged 1.3 and 1.2, respectively, and CPUE of fish aged 2.3 in the Copper River district fishery during 1983 (bottom frame) and 1984 (top frame). Boat-days is the unit of effort.

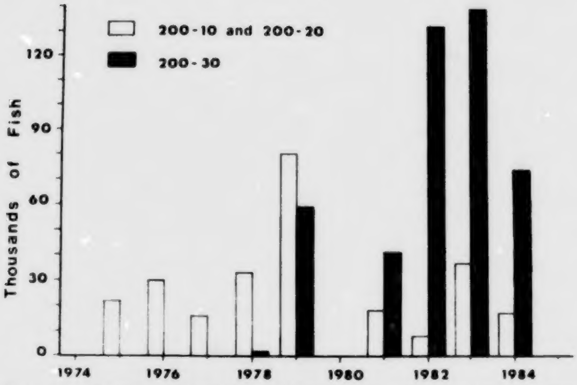

FIG. 11. Catches of sockeye salmon from the nearshore fishery (subdistricts 200-10 and 200-20) and from the offshore Kayak Island Fishery (subdistrict 200-30) for the years 1974 to 1984.

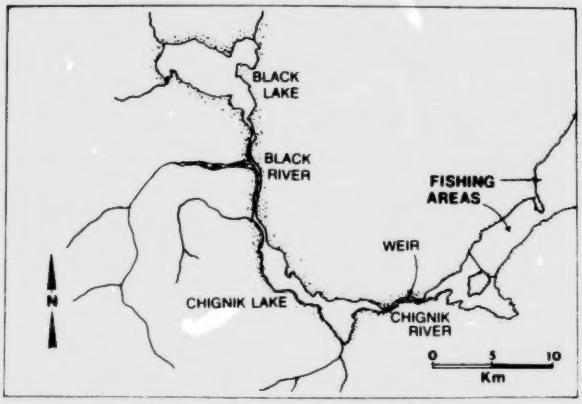

FIG. 12. The Chignik and Black lakes area showing the location of the fishery and the major sockeye salmon spawning drainages.

ging. Tags were recovered during foot surveys of spawning areas. The fraction of all tags of a particular color code recovered in Chignik Lake gives an estimate of the fraction of escapement that comprised late run fish during the period when tags of that color were applied.

A logistic curve fit to these fractions (see Fig. 13) is a time-of-entry (TOE) curve. An average TOE curve calculated from 1962 to 1966 was used to apportion historic data into component runs, to set escapement goals for each run, and to regulate the fishery to attain these goals. Calculations are most accurate when the early and late runs have (1) the same variance in their migratory time density function (Mundy 1982), (2) different mean dates with little variation among years, (3) equal magnitude, and (4) the same age composition or no differences in migratory timing by age (Burgner and Marshall 1974; Marshall and Burgner 1977).

SPA AS TEST AND SOLUTION

Although there has been no recent tagging to evaluate the strict application of the average TOE curve, annual TOE curves have been built after each fishing season with SPA of samples from spawners and from catches taken from 1978

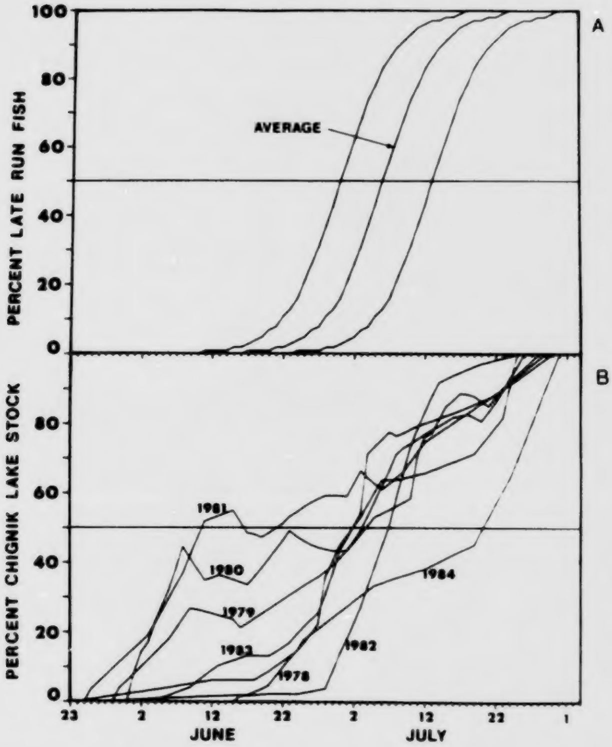

FIG. 13. Earliest, latest, and computed average time-of-entry curves from the Chignik sockeye salmon runs based on adult tagging conducted from 1962 to 1966 (frame A); and daily stock composition estimated by SPA for the years 1978 to 1984 (frame B). Both frames refer to the same run.

to 1984 (Conrad 1982, 1984a, and 1984b; and Conrad and Ruggerone 1985). Variation of the SPA-computed TOE curves for 1978-84 was much larger than the variation from 1962 to 1966 (Fig. 13); dates on which catches changed from mostly early, to mostly late run fish ranged from 21 June to 21 July during 1978-84 and the variances of the migratory time-density functions for each run were significantly different in all years but one (Table 4).

The dramatic variation among annual TOE curves is due to differences in magnitudes, age compositions, and migratory time densities by age between the two runs. Estimated stock size has varied dramatically during the period 1978 to 1984 (Fig. 14). The Black Lake run had been less stable, ranging from approximately 560 thousand in 1980 to approximately 3.2 million in 1984 (Fig. 14). The effect of numerical swamping is manifested in extremely skewed entry patterns (see Fig. 13). Larger runs to Chignik Lake (the late run) in 1979, 1980, and 1981 correspond to TOE curves much earlier than the average while smaller runs in 1982 and 1984 correspond to TOE curves that are much later. Also, because age composition varied considerably between runs, among years (Table 5), and within samples drawn from the fishery (Fig. 15), annual TOE varied according to the strength of different year-classes from the two runs.

Because of the extreme annual variation in TOE, SPA is now used to generate annual TOE curve for the Chignik fishery (Marshall et al. 1980). Each year scales are collected

TABLE 4. Mean and variance of the migratory time-density of Black and Chignik lakes returns as estimated by SPA, 1978-84. The test is for equal variances.

	Black Lake		Chignik Lake		
Year	Mean	Variance	Mean	Variance	*F*-Test
1978	21 June	138.9	18 July	212.8	1.53 *
1979	26 June	206.3	18 July	254.8	1.24
1980	2 July	126.0	18 July	297.3	2.36 **
1981	20 June	199.3	7 July	385.6	1.93 **
1982	22 June	37.6	31 July	543.1	14.44 **
1983	22 June	125.9	21 July	320.7	2.55 **
1984	18 June	109.1	16 July	695.9	6.38 **

* Significant when probability of a Type I error is set at 0.05.
** Significant when probability of a Type I error is set at 0.01.

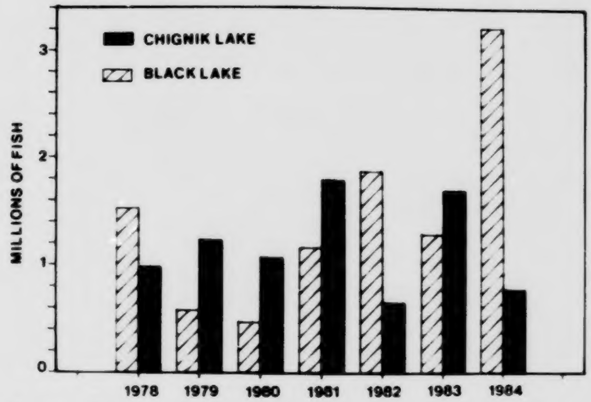

FIG. 14. Total return of sockeye salmon, by stock, to the Chignik River system as estimated through SPA for the years 1978 to 1984.

TABLE 5. Age composition of Black (BL) and Chignik (CL) lakes returns as estimated by SPA, 1978-84.

		Percent composition by stock				
Year	Lake	1.2	2.2	1.3	2.3	Other[a]
1978	BL	3.3	7.9	49.3	38.4	1.1
	CL	1.9	17.0	5.6	70.6	4.9
1979	BL	3.4	19.8	20.8	54.7	1.3
	CL	1.9	15.6	8.4	72.8	1.3
1980	BL	9.2	11.5	14.9	63.3	1.1
	CL	5.6	17.5	11.7	64.1	1.1
1981	BL	4.9	2.0	54.9	36.7	1.5
	CL	2.9	5.2	42.8	47.5	1.6
1982	BL	2.8	0.6	87.0	7.0	2.6
	CL	2.2	7.9	20.6	66.1	3.2
1983	BL	38.0	4.4	31.9	24.0	1.7
	CL	5.4	16.7	13.6	63.3	1.0
1984	BL	2.6	1.5	83.2	9.2	3.5
	CL	2.1	4.5	45.4	44.8	3.2

[a] Includes fish aged 1.1, 0.3, 2.1, 1.4, 3.2, 2.4, and 3.3.

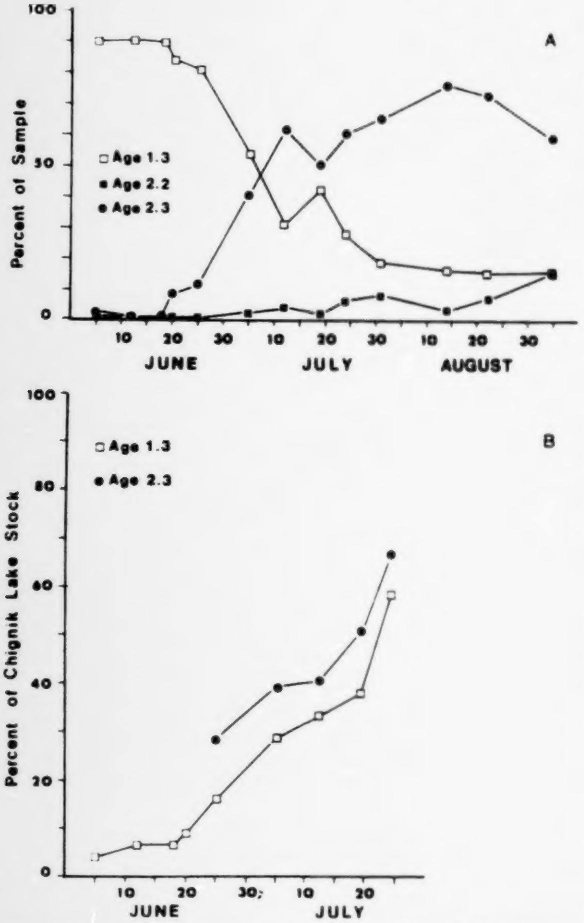

FIG. 15. Temporal trends in age composition of the sockeye salmon run to Chignik during 1984 as determined by catch sampling (Frame A); and temporal trend in the stock composition of selected age classes smoothed by a 3-day moving average (frame B).

from Black Lake in June well before the Chignik run is present in the fishery. Early maturing fish from the same brood year are used to represent Chignik Lake; for instance, fish aged 1.2 maturing in 1985 have the same lacustrine history of growth as fish aged 1.3 maturing in 1986. The decision rule and correction matrix are built on these two representations then applied during the fishery to scale samples taken from catches. When estimated proportions from the SPA indicate a significant shift from early to late run in the fishery, management emphasis begins for the late run, and ends for the early run. By using SPA in this way to directly estimate time-of-entry, considerable error can be avoided in deciding when to switch emphasis from one to the other run in the Chignik fishery.

Lynn Canal

From 1976 to 1985, the drift gillnet fishery in Lynn Canal (Fig. 16) caught an average of 203 000 sockeye salmon annually. By regulation, the fishery usually starts on the third Sunday of June and continues through mid-October with typically 2–3 days of fishing each week. The management objectives are to attain specific escapements to each of the Chilkat and Chilkoot rivers and to achieve weekly catches which are proportional to stock size throughout the season. To meet these objectives, prompt precise in-season information on run strength is needed. Because sockeye salmon average 2 and 30 days in travel from the fishery to weirs below Chilkoot and Chilkat lakes, respectively, run strength (particularly for the Chilkat) is estimated in-season from catch and effort statistics rather than by counting escapements.

High variance in CPUE statistics means low precision in forecasts. Environmental factors (Sheridan 1962; Mundy 1982), salmon behavior in the fishing area (Schnute and Sibert 1983), estimation of fishing effort (Hilborn and Ledbetter 1985), and differences in migratory timing among component stocks (Walters and Buckingham 1975) are common sources of variablility in salmon CPUE statistics. Forecasts are improved when they are stratified according to significant sources of variation in these statistics. We therefore tested the hypotheses that stocks, as identified through SPA, and age of returning sockeye salmon significantly affected variation in CPUE statistics for fish migrating through Lynn Canal from 1981 through 1985.

An unbalanced analysis of covariance in a 2×3 factorial model with interaction is the chosen experimental design. Estimates of catch by age and river of origin were derived through SPA (Marshall et al. 1982; McPherson et al. 1983; McPherson and Marshall 1986), and boat-days were selected as estimates of effort. Both catch and effort were summed over days within each week for calculating weekly CPUE. In the analysis, the fraction of the cumulative CPUE by week,

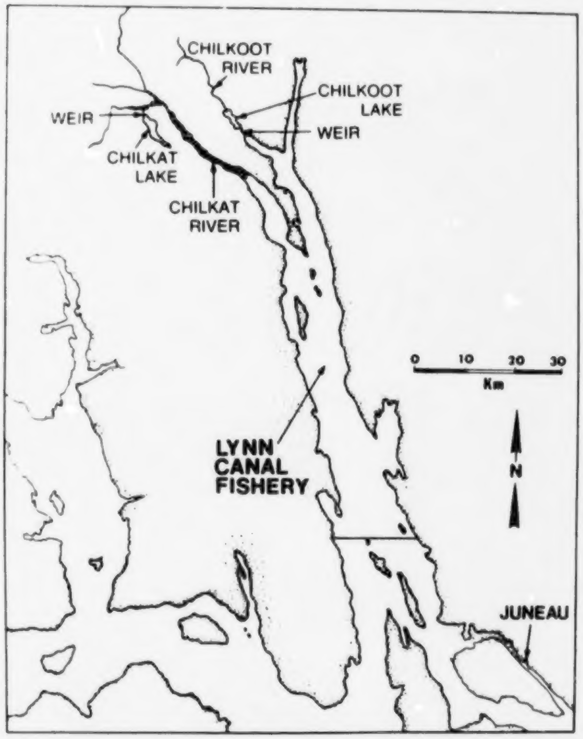

FIG. 16. The Lynn Canal area showing the location of the fishery and the major sockeye salmon spawning drainages.

river, age, and year is the dependent variable (y) and river of origin and age are the main effects with one river-by-age interaction. Weeks is the covariate (x); years are the replicates. Levels of the river factor are Chilkoot vs. Chilkat and levels of the age factor are ages 1.3 vs. 2.2 vs. 2.3. Weeks are sequentially numbered with "1" assigned to the week beginning on the third Sunday in June. Because cumulative CPUE as a function of weeks is generally sigmoid (Fig. 17), the transformation $y' = \ln|1/y - 1|$ was used to obtain linearity where y is the weekly fraction of cumulative CPUE (Mundy 1982). The transformation is based on the logistic equation $f(x) = y = [1 + a \exp[-bx]]^{-1}$. When $y = .5$, $X = (\ln a)/b$ = MT(50) and when $f(x{:}y=.5) = b/4$ = MT(slope) where MT(50) is the date half the run was passed (the mean date of migration of Mundy 1982), and MT(slope) is the speed at which the run was passing through the fishing district during MD(50). Because y is undefined whenever $y=1$ or $y=0$, early weeks when no salmon had yet been caught and/or late weeks when all the catch had been made were dropped from the analysis. Because of these missing values, an unbalanced design based on the procedures for General Linear Models (Searle 1971) was used. Least-square means (population marginal means) were calculated for all levels of major factors and their interaction (Searle et al. 1980).

The analysis of covariance shows that from 1981 to 1985 age and river represent highly significant sources of variation in the CPUE statistics (Table 6). The general linear model explains just over 90% of the total variation with the covariate (weeks) making up most of the variation (about 81%). The factors of age, river, and their interaction account for just over half of the remaining variation.

Adjusted least-square means of CPUE (Table 6) indicate the order in which the majority of fish in each age group appear in the catch. For instance a group mean value of zero indicates no difference in arrival in the fishery compared to the data for all groups combined; a negative value indicates early arrival while a positive value indicates late arrival. These data show that Chilkoot fish arrive earlier than Chilkat fish. Among age classes, fish aged 1.3 arrive first followed by those aged 2.3 and 2.2. When stocks are analyzed separately, the sequences order holds only for the Chilkat fish; two-freshwater (2.2 and 2.3) Chilkoot fish return at the same time. Because some deviation in the order of migration is evident (Table 7), these conclusions should be treated as tendencies, not certainties.

Stratification of CPUE statistics by age and river of origin is an important first step toward removing variation due to differences in migratory timing between the two stocks.

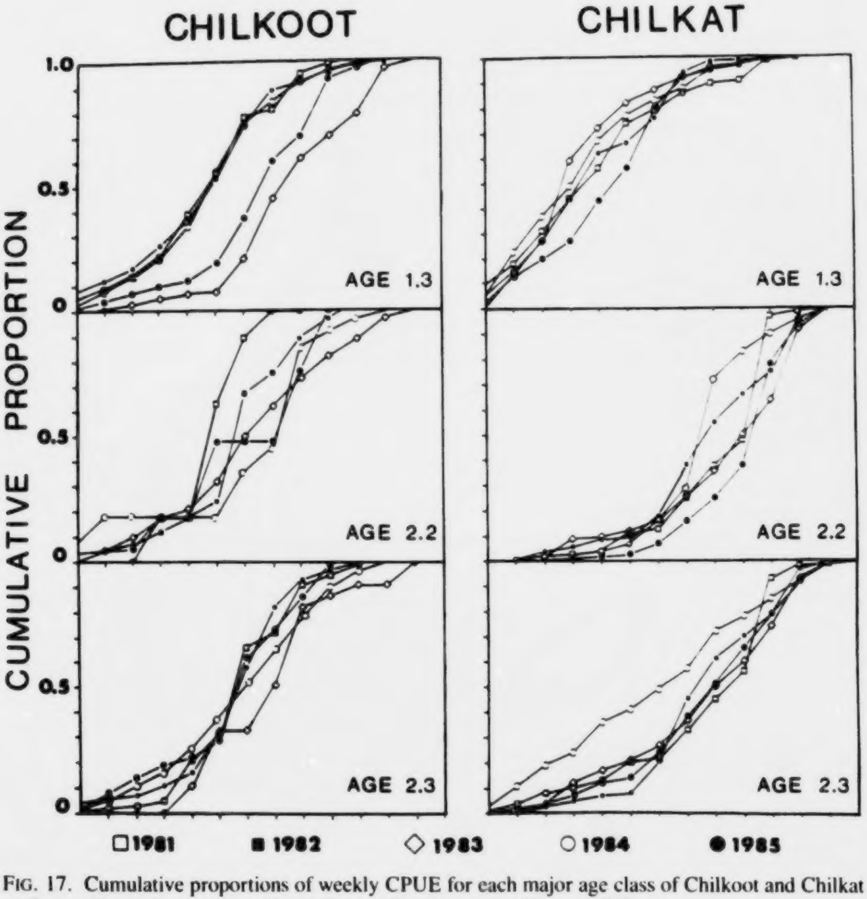

FIG. 17. Cumulative proportions of weekly CPUE for each major age class of Chilkoot and Chilkat sockeye salmon in the Lynn Canal fishery for the years 1981 to 1985.

TABLE 6. Tests of the significant effects of age and river of origin on the CPUE statistics of sockeye salmon caught in the Lynn Canal drift gillnet fishery from 1981–85. Normalized, cumulative CPUE is the dependent variable. Single asterisks (*) connote .01 < probability of a Type I error <0.05; double asterisks (**) connote probability of a Type I error <0.01.

			Analysis of covariance						
			Sequential		Partial				
	df	SS	SS	*F*	SS	*F*	MS	*F*	R^2
Model	6	1 557					260	490	0.905
Age	2		108	102	161	152			
River	1		<1	1.8	20	38			
River/Age	2		54	51	93	88			
Weeks	1		1 394						
Error	308	163					<1		
Total (Corrected)	314	1 720							

Least-square means

			LS MEAN	SE	*P*(t:Ho:LsMean=0)
River	Chilkoot		−0.01	0.06	0.87
	Chilkat		0.51	0.06	**
Age	1.3		−0.75	0.07	**
	2.2		0.95	0.08	**
	2.3		0.53	0.07	**
River by Age	Chilkoot	1.3	−0.24	0.10	*
	Chilkoot	2.2	0.17	0.11	0.13
	Chilkoot	2.3	0.04	0.10	0.69
	Chilkat	1.3	−1.25	0.10	**
	Chilkat	2.2	1.73	0.10	**
	Chilkat	2.3	1.02	0.10	**

These factors represented about half of the variation in CPUE statistics not attributed to the covariate (weeks). Although this analysis is mute on what form algorithms for in-season forecasting should take, such algorithms will be far more accurate if they incorporate differences in river of origin and age.

The Transboundary Rivers

TREATY

The Treaty between the Government of the United States of America and the Government of Canada concerning Pacific salmon, signed at Ottawa, January 28, 1985, entitles Canadian fishermen to harvest 15% of the total allowable catch (TAC) of sockeye salmon from the Taku River and 35% or 10 000 sockeye salmon (whichever is the greater number) of the TAC for the Stikine River. Because sockeye salmon bound for both rivers are caught in mixed-stock fisheries along with sockeye salmon not included in these entitlements, SPA is used to estimate catch by stock for both rivers during and after each fishing season and, for the Stikine River, to estimate sockeye escapement also.

TAKU RIVER

Since 1979 the drift gillnet fishery in Alaska District 111 (Port Snettisham, Stephens Passage and Taku Inlet) and the Canadian gillnet fishery in the river, have annually caught an average of 82 000 and 15 000 sockeye salmon, respectively (McGregor 1985) (see Fig. 18 for locations). In 1985, the fishery in District 111 was managed according to the results of SPA for previous years (Don Ingledue, personal communication, P.O. Box 20, Douglas, Alaska 99824). Preliminary statistics indicate that 87 100 fish were caught in District 111, 14 244 fish were caught in the Canadian fishery, and 107 000 escaped to spawn. Post-season estimates from SPA indicate that in 1983 75.5%, and in 1984 75.8% of the catch in District 111 had been Taku River fish (McGregor 1986). If the mean of these estimates (75.65%) is found to be an accurate measure for 1985, the Canadian catch in the river fishery will have been slightly (2.78%) above the allowable 15% and the escapement will have exceeded the goal of 71 000 to 80 000 set by the Transboundary Technical Committee (1984). Scale patterns analysis of data collected in 1983 and 1984 shows that fish bound for the Taku River were present during all fishing periods from June through August (Fig. 19). However, the percent of these catches bound for the Taku River were often lower in July than in June or August. Information on the route of salmon migration through the district will be available in 1986 after scales are collected from all the subdistricts of District 111.

Although SPA and stock-specific fishery management has not yet been used within the Taku River, the potential to do so exists. Radio-telemetry and tagging studies (Transboundary Technical Committee 1984; Clark et al. 1986) show

TABLE 7. Results of linear regressions of the logarithmic transformation of cumulative CPUE against weeks by year, by age, and by river of origin. MT(50) is a measure of timing of the migration while MT(Slope) is a measure of the speed (see the text to find how these statistics were calculated.)

	Chilkoot River			Chilkat River		
	1.3	2.2	2.3	1.3	2.2	2.3
1981						
Number	10	4	11	11	11	13
r-square (%)	96.6	89.9	98.5	95.6	89.1	91.5
MT(50)	5.3	5.6	6.6	4.6	8.4	7.8
MT(Slope)	0.20	0.32	0.23	0.14	0.21	0.17
1982						
Number	11	10	10	11	12	11
r-square (%)	98.0	95.0	95.9	98.1	96.5	96.6
MT(50)	5.2	6.3	6.2	4.5	8.6	8.4
MT(Slope)	0.18	0.19	0.20	0.18	0.16	0.18
1983						
Number	11	8	11	10	11	11
r-square (%)	69.8	93.8	97.9	97.7	45.2	54.2
MT(50)	6.4	7.6	6.8	4.1	10.0	8.7
MT(Slope)	0.10	0.16	0.14	0.16	0.09	0.09
1984						
Number	11	11	11	11	11	12
r-square (%)	99.1	82.8	98.7	98.5	97.4	96.9
MT(50)	5.6	6.5	6.6	4.2	8.4	6.9
MT(Slope)	0.19	0.13	0.17	0.16	0.20	0.12
1985						
Number	11	8	11	11	9	11
r-square (%)	96.3	92.6	93.4	98.3	96.4	98.8
MT(50)	7.1	7.2	5.9	5.2	9.8	8.7
MT(Slope)	0.18	0.15	0.20	0.19	0.22	0.15

that there are differences in migratory timing among the major stocks through the lower river. We have found that age composition of lower river catch samples accompany the changes in stock composition (McGregor and McPherson 1986, McGregor et al. 1984). Also, fish aged 1.3 from Kuthai and Little Trapper lakes have had distinctly different scale patterns (McGregor et al. 1983).

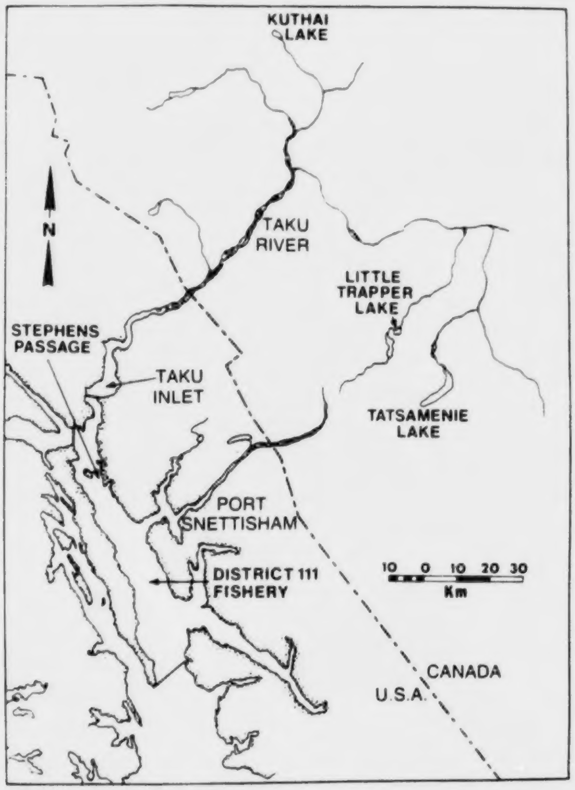

FIG. 18. The Taku-Snettisham area showing the major spawning drainages and fishing area.

STIKINE RIVER

Since the mid-1970's, the drift gillnet fishery in Alaska Districts 106 and 108 (Sumner and Clarence straits) has annually caught an average of 91 000 sockeye salmon while the Canadian gillnet fishery in the river has caught an average of 21 000 sockeye (Transboundary Technical Committee 1984) (see Fig. 20 for locations). Preliminary SPA of data collected from District 106 during 1985 shows that Tahltan Lake stocks were more abundant in Sumner Strait (subdistrict 41) than Clarence Strait (subdistrict 30) while fish from other stocks were about as likely to be found in one subdistrict as the other (Fig. 21). Comparison of CPUE among weeks shows that sockeye salmon bound for the Nass and Skeena rivers increased in abundance as the season progressed, while abundance of fish returning to Tahltan Lake declined after mid-July. The Tahltan Lake stock also passed through the inriver fishery earlier than other stocks in the Stikine River (Fig. 22).

Scale patterns analysis of Canadian river fishery catches and weir counts of sockeye salmon returning to Tahltan Lake (Fig. 20) were used to estimate the entire escapement of sockeye salmon to the Stikine River (Oliver et al. 1985).

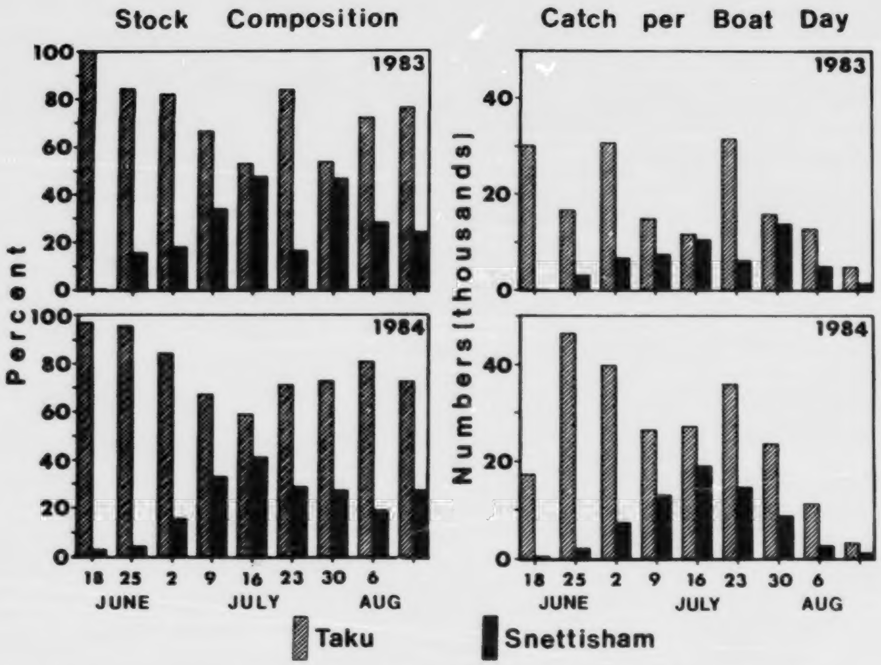

FIG. 19. The percent of weekly sockeye salmon catches in District 111 contributed by Taku River and Port Snettisham stocks, respectively, and the corresponding CPUE for the years 1983 and 1984. The last bar in each graph is a mean value for catches in fishing periods after mid-August.

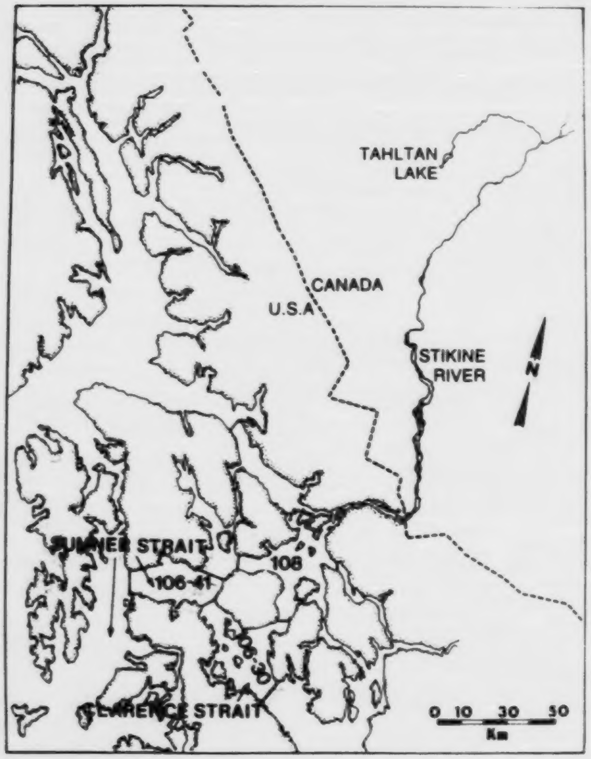
TAHLTAN LAKE
CANADA
U.S.A.
STIKINE RIVER
N
SUMNER STRAIT
106-41
106
CLARENCE STRAIT
0 10 30 50
Km

FIG. 20. The Sumner Strait–Stikine area showing the offshore fishing areas, 106-41 and 106-30.

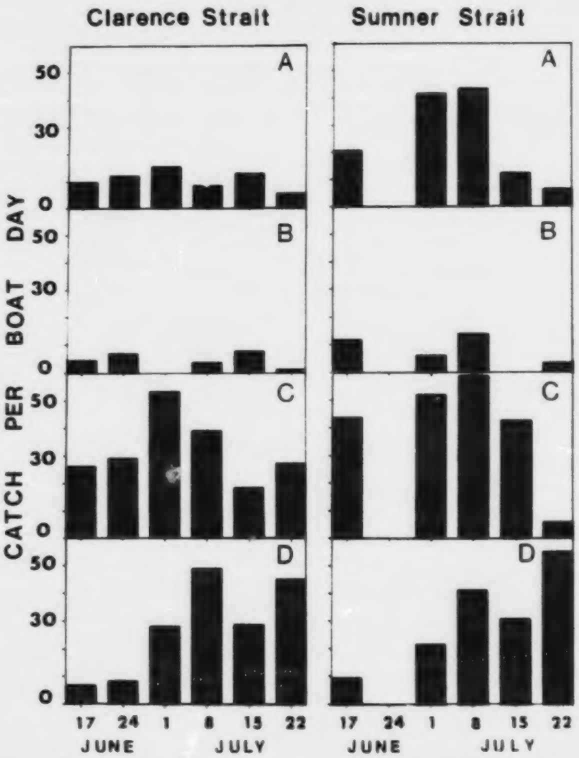

FIG. 21. Weekly CPUE for four stocks in the 1985 Clarence Strait (subdistrict 30) and Sumner Strait (subdistrict 41) fisheries. Stock groupings are (A) Tahltan, (B) other Stikine, (C) Alaska, and (D) Nass and Skeena rivers.

TABLE 8. Catch, escapement, exploitation rate, and total return of Tahltan and other stocks of Stikine River sockeye salmon, 1982–84.

Description	Stock	1982		1983		1984	
		Number	%	Number	%	Number	%
Sumner/Clarence straits catch	Tahltan			5 030	10	3 648	3
	Stikine	37 562[a]	19	633	1	5 487	4
	Nass/Skeena	61 976	32	10 610	22	26 477	27
	Alaska	37 635	49	32 670	67	62 603	66
Stikine Delta[b] catch	Tahltan	4 128	63	77	44	719	50
	Stikine	2 425	37	99	66	719	50
Canadian commercial catch	Tahltan	9 679	63	7 247	44	0[c]	
	Stikine	5 685	37	9 224	66	0	
Canadian subsistence[d] catch	Tahltan	4 453	90	4 184	90	4 794	90
	Stikine	495	10	465	10	553	10
Escapement	Tahltan	28 257	59	21 256	36	32 777	50
	Stikine	19 803	41	38 521	64	33 213	50
Exploitation rate (%)	Tahltan	ND		43.8		21.8	
	Stikine	ND		21.3		16.9	
	Total	57.3		31.1		19.4	
Total return	Tahltan	ND		37 794		41 938	
	Stikine	ND		48 942		39 972	
	Total	112 487		86 736		81 910	

[a] In 1982 stock contribution rates were estimated for all Stikine stocks as a group.

[b] Stikine Delta catch assumed to be 100% of Stikine stocks and are allocated in the same proportions as the Canadian commercial catch.

[c] There was no Canadian commercial fishery in 1984, stock proportions derived from test fishery samples.

[d] Assumed to be 90% Tahltan and 10% other Stikine stocks.

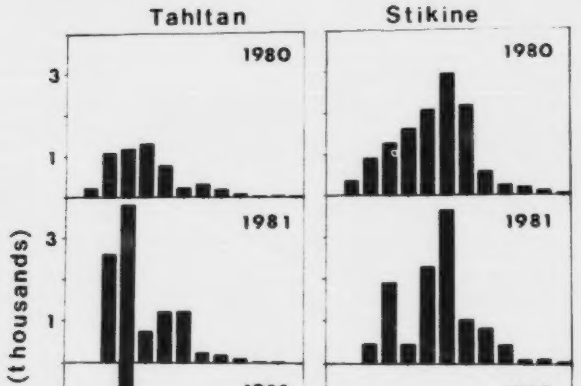

FIG. 22. Catch of sockeye salmon that originated from Tahltan Lake and other "Stikine" River areas taken in the Stikine River by Canadian commercial fishermen during the years 1980 to 1983.

When sockeye salmon are classified as those bound for Tahltan Lake and those not, and one assumes that all stocks suffer equal weekly exploitation rates in the river commercial fishery (Table 8), the return to Tahltan Lake (weir counts plus catch) divided by the fraction of the catch in the lower river that was bound for Tahltan Lake is an estimate of the escapement past Districts 106 and 108.

In 1985, SPA on scales collected during the fishery indicated a return to the Stikine River much larger than expected. Estimates of escapement and average maturity schedules were used to forecast a return of between 85 000 and 125 000 sockeye salmon, with a most probable return of 85 000 fish (Transboundary Technical Committee 1984). Since the Technical Committee set the escapement goal at 70 000 fish, the TAC was 15 000 to 55 000 fish. As the fishing season progressed in Districts 106 and 108, the CPUE remained higher than expected. Because fish bound for the Nass, Skeena, and Alaska rivers also caught in District 106 (Oliver et al. 1985; Hoffman et al. 1984), high CPUE did not necessarily indicate a larger than expected return of fish to the Stikine River. However, SPA conducted during the season did indicate higher than expected CPUE for sockeye salmon returning to the Stikine River. Accordingly, fishing time and fishing areas were expanded to increase catches. Preliminary post-season statistics from 1985 justify this decision and the reliance that was placed on the in-season SPA as a management tool; 122 000 sockeye salmon escaped to spawn while 68 500 were harvested, 44 000 (65%) in Districts 106 and 108 and 28 000 (35%) in Canadian fisheries as per the entitlements in the Treaty.

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In-Season Stock Identification of Sockeye Salmon (*Oncorhynchus nerka*) Using Scale Pattern Recognition

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Abstract

COOK, R.C., AND I. GUTHRIE. 1987. In-season stock identification of sockeye salmon (*Oncorhynchus nerka*) using scale pattern recognition, p. 327–334. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Automated video digitization of sockeye salmon scales was investigated as a technique to help meet the logistic requirements of in-season stock identification for the Fraser River. A microcomputer-based system with a television camera interface was used to make 64 000 luminance measurements on each scale in 6 seconds. The resulting data were converted to circuli spacing information for use in stock identification. Algorithms were established to allow for rapid discriminant analysis and stock composition estimation for any possible combination of Fraser River and Lake Washington stocks. The results of this feasibility study were then evaluated in the context of the management problem and the rapid advances in image processing technology.

Résumé

COOK, R.C., AND I. GUTHRIE. 1987. In-season stock identification of sockeye salmon (*Oncorhynchus nerka*) using scale pattern recognition, p. 327–334. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les auteurs ont étudié la numérisation automatisée sur magnétoscope d'écailles de saumon nerka afin de déterminer si cette technique permettrait de répondre aux besoins logistiques de l'identification saisonnière de stocks dans le fleuve Fraser. Un système composé d'un micro-ordinateur lié à une caméra de télévision a été utilisé pour effectuer 64 000 mesures de la luminance sur chaque écaille en 6 secondes. Les données obtenues ont été transformées en valeurs d'espacement des anneaux qui serviront à l'identification de stocks. On a calculé les algorithmes nécessaires à une analyse discriminante rapide et à l'estimation de la composition d'un stock pour toutes les combinaisons possibles de stocks provenant du fleuve Fraser et du lac Washington. Les résultats de la présente étude de faisabilité ont ensuite été évalués dans le contexte du problème de gestion et des progrès rapides des techniques de traitement des images.

Introduction

There have been many investigations of stock composition of sockeye salmon (*Oncorhynchus nerka*) populations in areas of intermingling. Some of the earlier studies were conducted to determine the continent of origin of sockeye taken by high seas fisheries (Anas 1964; Mason 1966; Anas and Murai 1969). These and later studies show that differences in the circuli patterns on scales are sufficient to identify both continent and region of origin (Cook et al. 1981; Knudsen and Harris 1982). Circuli data for sockeye scales taken from the component populations were used to develop discriminant rules capable of classifying sockeye salmon taken in the North Pacific study area. The success of these studies led to further applications with both high seas and inshore sockeye as well as other salmon populations (Myers et al. 1984; Conrad 1984; Marshall et al. 1984; Wilcock 1984; among others).

These studies were conducted a posteriori. Sampling from the component populations, to obtain training samples for estimating the discriminant rule, usually followed sampling from the mixed population to obtain unknown samples from which stock composition estimates were obtained for previous time periods. Training samples and unknown samples were usually taken from the same cohort because this controlled for and utilized the annual variability in scale patterns that occurs among stocks under differing ecological conditions (Konovalov 1971). However this a posteriori sampling plan would preclude mixing proportion estimation on the same day of sampling because the component stocks may not segregate into their rivers of origin and be available for training samples until later. For in-season management this segregation does not usually occur until the need for the estimates has passed. Annual variability may not be directly utilised to improve classification accuracy for in-season management because training samples and unknown samples must be taken from different cohorts. (Since smolts are subjected to selective mortality that will often affect scale measurement data they are a poor choice for training samples.) Scale pattern variability among stocks must be greater than variability among years, or indirect methods for assessing annual variability and correcting stock composition estimates must be developed.

In previous studies scale data were extracted by making meticulous measurements on circuli for a large number of sockeye scales. More recent studies have utilized digitizing tablets to record the circuli data; however, each circulus was still, by necessity, manually identified. Subjective judgments on the number of circuli comprising "summer" and "winter" growth zones were also made. To collect data on the numbers of scales needed for in-season management of the Fraser River sockeye fishery it was considered necessary to further automate the scale measurement process. This would considerably reduce the number of subjective judgments and provide more repeatable scale measurement data; however, it was also recognized that some valuable subjective data would no longer be available for stock identification.

To meet the logistic requirements for management of the Fraser River sockeye fishery it is necessary to collect and analyze the data very rapidly. Many stocks contribute to the fishery and each stock may have a different migration route with unique timing. Thus, the composition of the stock complex will vary. Some stocks will be extremely scarce at times and a very large number of multiple category discriminant analyses may be needed. For example, with five sockeye stocks, one five-category, and as many as 5 four-category, 10 three-category, and 10 two-category analyses (for a total of 26) could be required. With up to 10 major stocks, in any one year there are 1013 potential stock combinations. Thus, a statistical method is needed that is rapid enough to interactively estimate stock composition for any combination of stocks that may occur.

In this paper we present the results of feasibility studies conducted in late 1984 at the International Pacific Salmon Fisheries Commission (IPSFC) using a prototype microcomputer-based system and a television camera interface. The system was designed to measure lacustrine and early marine growth of Fraser River sockeye salmon. We propose that unsupervised estimation techniques be investigated as a method to assess and correct for annual scale pattern variability. Unsupervised estimation allows the training samples and the resulting discriminant rule to be modified by the unknown samples collected during the current season. We also propose that improved microcomputer systems be employed for data acquisition.

Methods and Materials

Scales were measured from 13 stocks in the 1981 Fraser River escapement and from the single Lake Washington stock. The data were examined for variability among stocks using graphical methods and discriminant analysis. We utilized likelihood ratio classification procedures (Smith 1947) to allow interactive discriminant analysis and stock composition estimation. Results are presented for the classification for several important stock combinations.

A microcomputer equipped with a successive approximation converter (i.e., low end video digitizer) was used to digitize a standard RS-170 video signal. A closed circuit television camera mounted on a microscope provided the video image of a sockeye scale on a closed circuit monitor. A vertical line on the surface of this monitor allowed the operator to properly orient the scale in the field of view. The video digitizer then loaded the image into microcomputer memory in about 6 seconds. The digital image consisted of luminance measurements in a 256 by 256 array. Each point in the array (termed a pixel) contained a luminance measure. Luminance was coded as an 8-bit integer representing one of 256 possible shades of gray (0–255). Luminance values were extracted for 200 pixels along a preset line originating at the focus (center) of the scale and continuing along the longest axis of the scale for a distance of 1.0 mm (Fig. 1). This distance was sufficient to contain measurement data from the entire lacustrine and early marine growth zones. The computer was programmed to interrogate data files containing information on scale number, age, sex, body length, weight, and other biological data. The user was then prompted for the scale card and scale number required to construct a particular sample. Because body length differs among Fraser River sockeye stocks, length was entered on the data files along with digitized luminance values.

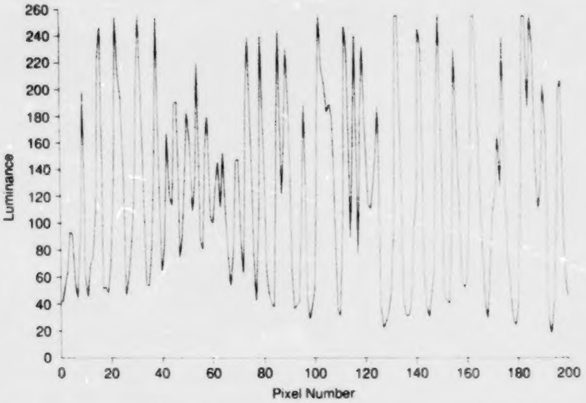

FIG. 1. Plot of 200 digitized luminance values from the focus along the longest axis for 1.0 mm on an example sockeye salmon scale.

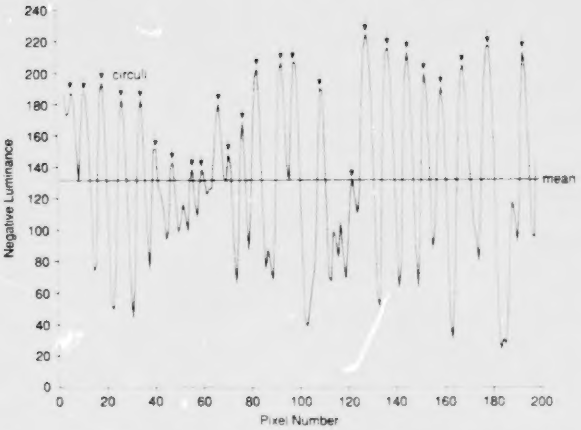

FIG. 2. Local maxima of filtered negative luminance values that were designated as circuli for the example sockeye salmon scale.

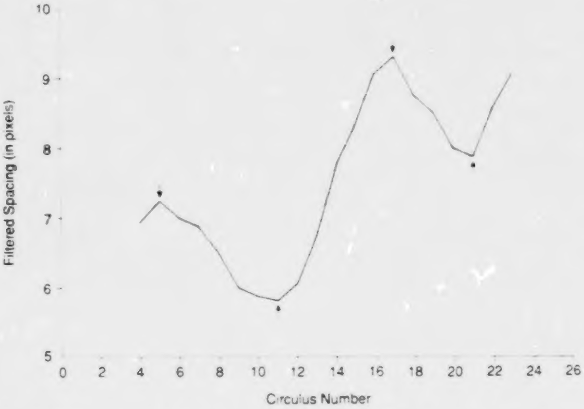

FIG 3. Filtered spacing data showing local minima and maxima corresponding to zones of closely and widely spaced circuli, respectively.

The extracted luminance values were then interpreted with a computer program to provide circulus spacing information. It would be intuitively satisfying if the program provided biologically meaningful variables similar to those obtained by subjective interpretation; however, for stock identification purposes variables need only differ consistently among stocks. A set of scales was assembled to represent the variety exhibited among the various stocks, and each scale was both digitized and photographed. The program was then interactively modified until the procedures provided variables that could be visually related to scales in the set by viewing each photograph. The net result was an interpretation program that provided consistent circuli counts and measures for the full set of photographs. The program also provided several variables that correlated strongly with the location of the end of the lacustrine growth zone; however, none of the algorithms was completely satisfactory for identifying this scale area. The development of the program was very subjective, being dominated by the authors perceptions and preconceptions, but the variables created with the final version were completely repeatable.

The algorithms were quite simple. The negative of the original luminance series was taken (255 minus the original luminance) so that maxima would correspond to the darker circuli. This result was then smoothed with a weighted moving average (Fig. 2) using the following expression to obtain a new luminance value for a pixel, L_i:

$$L_i\ (\text{new}) = (L_{i-2} + 3L_{i-1} + 6L_i + 3L_{i+1} + L_{i+2})^{1}/_{14}$$

The successive weights used were 1, 3, 6, 3, and 1. The mean was then calculated and certain circuli were designated as local maxima. The criterion for a local maxima was that its luminance value must exceed the mean and exceed the two previous and two subsequent values in the series. The spacing between the circuli thus identified was calculated and weighted by a moving average with successive weights of 1, 2, 3, 4, 3, 2, and 1 (Fig. 3). Local minima and maxima were then recorded to obtain the locations of closely spaced and widely spaced circuli. This method has been used to identify annuli (Koo 1962). Before smoothing, the spacings were also used to identify variables representing rapid increases and decreases in the spacing regime. For each circulus the ratio of the distance across the preceding three circuli to the distance across the subsequent three circuli was calculated. The locations and magnitudes of the largest and smallest ratios were then recorded. Table 1 summarizes the variables that were created for each scale from the extracted luminance values.

TABLE 1. Scale measurement variables derived from digitized luminance values.

No.	Description
1–3	Circuli count to the 1st, 2nd, and 3rd least local minima in smoothed spacing.
4–6	Distance to the 1st, 2nd, and 3rd least local minima in smoothed spacing.
7–9	Circuli count to the 1st, 2nd, and 3rd greatest increase in smoothed spacing.
10–12	Distance to the 1st, 2nd, and 3rd greatest increase in smoothed spacing.
13–15	Circuli count to the 1st, 2nd, and 3rd local minima in smoothed spacing.
16–18	Distance to the 1st, 2nd, and 3rd local minima in smoothed spacing.

TABLE 1. (*Continued*).

No.	Description
19–21	Circuli count to the 1st, 2nd, and 3rd increase in smoothed spacing.
22–24	Distance to the 1st, 2nd, and 3rd increase in smoothed spacing.
25–27	Circuli count to the 1st, 2nd and 3rd least local maxima in smoothed spacing.
28–30	Distance to the 1st, 2nd and 3rd least local maxima in smoothed spacing.
31–33	Circuli count to the 1st, 2nd and 3rd greatest decrease in smoothed spacing.
34–36	Distance to the 1st, 2nd, and 3rd greatest decrease in smoothed spacing.
37–39	Circuli count to the 1st, 2nd, and 3rd local maxima in smoothed spacing.
40–42	Distance to the 1st, 2nd, and 3rd local maxima in smoothed spacing.
43–45	Circuli count to the 1st, 2nd, and 3rd decrease in smoothed spacing.
46–48	Distance to the 1st, 2nd, and 3rd decrease in smoothed spacing.
49	Distance from focus to circulus 2.
50–63	Distance from circulus 2 to 4, 4 to 6, ..., and 28 to 30.
64	Body length.

Notched box and whisker plots (Tukey 1977; McGill et al. 1978) were used to examine the differences among stocks (Fig. 4). For each category or stock a box was plotted which covered the middle 50% of the respective values. The center line shows the median, and the notches on the sides of the box allow pairwise comparisons. Pairs having notches with any overlap indicate no significant differences of medians at the 95% level. The "whiskers" on each box cover those points that are within 1.5 times the interquartile range beyond the box. Values beyond that range are plotted individually. The horizontal width of the box is proportional to sample size. These plots were used to select variables from the measured scale features for use in discriminant analyses.

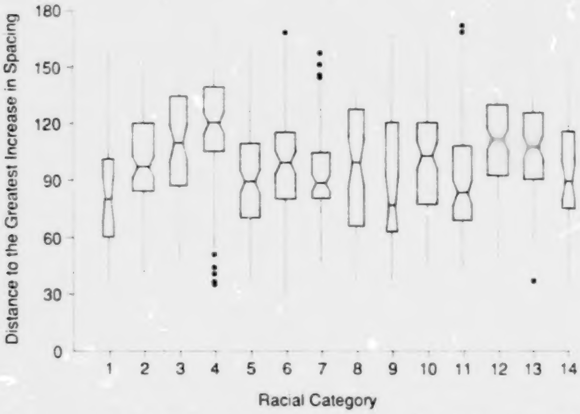

FIG. 4. Notched-Box-and-Whisker plots for the distance to the greatest increase in spacing for the 14 racial categories.

Some plots showed highly significant differences and were good candidates for discriminant analysis. An example was the variable described as "distance to the greatest increase in spacing" (Fig. 4). The differences are less apparent for the "distance from circulus number 6 to 8" (Fig. 5). Figures 4 and 5 represent the extremes seen in inter-stock variability among plots of the 64 variables examined. Variable numbers 4, 10, 16, 28, 40, and 49 through 64 were selected for discriminant analysis on the basis of their highly significant differences. It remains to determine whether this variable set will be sufficient for all stock combinations.

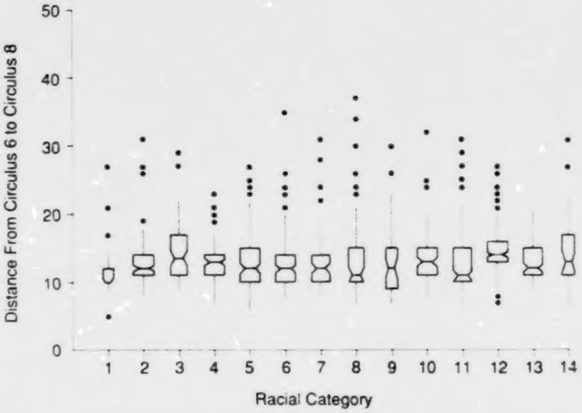

FIG. 5. Notched-Box-and-Whisker plots for the distance from circulus 6 to circulus 8 for the 14 racial categories.

The discriminant analysis was conducted by modifying established procedures as follows: For each stock a number of scales were measured to provide a set of training samples. These "standards" were then used to estimate the parameters required for discrimination and to evaluate the performance of the classification procedures. For this, the likelihood ratio test for two multivariate normal distributions (Welch 1939) was extended from the formulations of Lachenbruch (1967) for multiple category classification. The matrix form of the decision rule used in this study was:

$$\begin{aligned} \mathbf{D}_{rm}{}^{a} &= 1 \text{ if } \mathbf{F}_{rm}{}^{a} \geq \mathbf{F}_{sm}{}^{a} \text{ for all } s \neq r, \\ &= 0 \text{ otherwise.} \end{aligned}$$

The (r,m)th element of $\mathbf{D}^a$ is an array of 0's and 1's for each training sample a. There is one row in $\mathbf{D}^a$ for each measurement vector (or each fish scale). There is one column in $\mathbf{D}^a$ for each stock. Each row of the array contains a single 1 in the column to which that specimen has been classified. Thus, each $\mathbf{D}^a$ contains all classification results for the training sample from category a. Similarly the (r,m)th element of $\mathbf{F}^a$ is the value of the estimated multivariate normal density function for the rth fish from the ath training sample using the estimated density function for stock m.

Once the $\mathbf{F}^a$ are estimated from the training samples, all possible combinations of stocks can be considered in a computationally efficient manner. By deleting a column from all $\mathbf{F}^a$ before applying the decision rule the corresponding stock may be ignored. Of course, the computationally intensive operations required to obtain the $\mathbf{F}^a$ must have already been conducted. These computations need only be done once, prior to the beginning of the season. Further it is a simple matter to obtain the classification array from the $\mathbf{D}^a$. The classification array is required to obtain stock composition estimates from the results of classifying individuals (Worlund and

Fredin 1962; Pella and Robertson 1979; Cook 1982, 1983; and Grassia and Sundberg 1982). Classification arrays are presented for several important stock combinations in the results section.

The leaving-one-out procedure of Lachenbruch (1967) was used to evaluate the performance of the classification procedure and to obtain nearly unbiased estimates of the elements of the classification array. This required that the training sample means and the inverse of the pooled training sample variance-covariance matrix be adjusted for the omission of a single observation (fish scale) whenever m equaled a in **F**. Lachenbruch (1967) used Bartlett's (1951) mathematical identity to conveniently incorporate these recalculations into the coefficients for a two category discriminant function. With slight modifications of his formulae, it is possible to obtain a correction for the inverse matrix alone so that multiple category discrimination can be conducted. It is a simple matter to adjust the vectors of means for training sample a:

$$\bar{\mathbf{x}}_{a(j)} = \bar{\mathbf{x}}_{aj} - \bar{\mathbf{x}}_{aj} - \bar{\mathbf{x}}_{a}) / (n_a - 1)$$

where $\bar{\mathbf{x}}_{a(j)}$ is the training sample mean for category a after omitting scale measurement vector j, $\mathbf{x}_{aj}$ is the vector of scale measurement data to be omitted, n_a is the training sample size for stock a, and $\bar{\mathbf{x}}_a$ is the training sample mean for category a. The matrix inverse correction is given by:

$$\mathbf{S}_{(j)}{}^{-1} = \frac{n-2}{n-1}\left\{\mathbf{S}^{-1} + \frac{c\mathbf{S}^{-1}\mathbf{u}_j\mathbf{u}_j'\mathbf{S}^{-1}}{1 - c\mathbf{u}_j'\mathbf{S}^{-1}\mathbf{u}_j}\right\}$$

where $\mathbf{S}_{(j)}{}^{-1}$ is the variance–covariance matrix after omitting scale measurement vector j, n is the pooled training sample size, $c = n/(n-1)^2$, $\mathbf{u}_j = \mathbf{x}_{aj} - \bar{\mathbf{x}}$, and $\bar{\mathbf{x}}$ is the pooled training sample mean.

Results

It has long been recognized that scale patterns differ among the Fraser River sockeye salmon stocks (Gilbert 1913), and a technique for utilizing these differences has been used to manage the sockeye for many years (Henry 1961). The 1985 cycle is historically the most difficult cycle to analyze because the scale patterns are very similar among the major stocks on this cycle (J.C. Woodey, personal communication, IPSFC, P.O. Box 30, New Westminster, B.C. V3L 4X9). The return in 1981 was exceptionally difficult: scale pattern differences were not visually apparent and Henry's (1961) methods did not perform satisfactorily (J. Gable, personal communication, IPSFC, P.O. Box 30, New Westminster, B.C V3L 4X9). It was of primary interest to examine the performance of the new techniques for this particularly difficult year.

Fourteen stocks were considered large enough in 1981 to warrant analysis. Table 2 lists the stocks, the streams supporting them, and the numbers of scales from age 4_2 adults used to construct the training samples. These scales were from the previous brood of the 1985 cycle.

Discriminant analyses were conducted for several stock combinations deemed important to the in-season management process. Pre-season run projections for 1985 were used to identify those stocks likely to constitute 5% or more of the returning adults on each of several given days (J. Cave, personal communication, IPSFC, P.O. Box 30, New Westminster, B.C. V3L 4X9). This was done to provide an objective selection of stock combinations.

TABLE 2. Sample composition for 14 sockeye salmon racial categories.

Category number	Stock	River system	Sample size
1	Lake Washington	Cedar River	29
2	Early Stuart	Driftwood River	55
		Kynock Creek	56
3	Nadina	Nadina River	72
4	Gates	Gates Creek	103
5	Horsefly	Horsefly River	103
6	Late Stuart	Middle River	33
		Tachie River	69
7	Chilko	Chilko River	83
8	Adams	Adams River	33
		Scotch Creek	26
9	Seymour	Seymour River	38
10	Stellako	Stellako River	98
11	Birkenhead	Birkenhead River	93
12	Weaver	Weaver Creek	111
13	Portage	Portage Creek	93
14	Lower Shuswap	Lower Shuswap River	41

TABLE 3. Classification array for the Lake Washington and Early Stuart Races.

	Correct decision	
Calculated decision	L. Washington	Early Stuart
L. Washington	29	0
Early Stuart	0	111
Standard sample sizes	29	111

The classification arrays are presented for several stock combinations in Tables 3 through 8. The desired and obtained classification accuracies are summarized in Table 9. Classification accuracy is the major component of variability in stock composition estimates (Cook and Lord 1978; Cook 1982). The goal was to obtain accuracies (desired accuracies of Table 9) sufficient to provide narrow confidence intervals on stock composition estimates. Accuracies midway between the levels of random chance and perfect were considered to be the minimum acceptable because they will generally provide confidence intervals sufficiently narrow for managerial decision making (provided sample sizes are adequate).

Conclusions and Recommendations

The microcomputer-based data acquisition and analysis system extracted luminance values to identify circuli and measure spacing on the scales of Fraser River sockeye salmon. The algorithms for interactive selection of categories in stock composition estimation were successful in providing virtually instantaneous results. To the extent that the natural scale features extracted from the video image differed among stocks, the system is capable of meeting the logistic requirements for in-season stock identification for the Fraser

TABLE 4. Classification array for the Lake Washington, Early Stuart, Nadina, Horsefly, and Late Stuart races.

Calculated decision	Correct Decision L. Washington	Early Stuart	Nadina	Horsefly	Late Stuart
L. Washington	28	0	0	0	0
Early Stuart	0	55	7	19	29
Nadina	0	12	48	2	26
Horsefly	1	20	1	62	22
Late Stuart	0	24	16	20	25
Standard sample sizes	29	111	72	103	102

TABLE 5. Classification array for the Horsefly and Late Stuart races.

Calculated decision	Correct decision Horsefly	Late Stuart
Horsefly	71	31
Late Stuart	32	71
Standard sample sizes	103	102

River. Unfortunately, the extracted scale features were sufficiently different for certain groupings and not for others.

To help improve accuracy, additional scale measurement data could be utilized. Since this feasibility study was conducted there have been major advances in image processing applications. It is now possible to obtain much more measurement data in a shorter time. It is also possible to interact with the data acquisition process and introduce subjective judgments. For instance, those complicated processes best performed by the human eye and mind that are largely repeatable can now be combined with fully automated procedures. Failures of the automated procedures can also be observed and corrected. This is not possible with the prototype system which has now been replaced with such a system. The number of potential scale features for use in discriminant analysis has been increased several-fold. Each potential scale feature would require a comprehensive analysis of variance to examine the effects of stock, year, and other relevant factors. The goal would be to obtain a variable set for which the effect of stock would be greater than the effect of year within cycles.

It is likely that the variables required to obtain sufficient classification accuracy will retain considerable yearly variability. Unsupervised estimation procedures have been devised to correct for training sample deficiencies and there is a considerable body of literature on the subject. A text by Patrick (1972) gives a good introduction to the subject and cites some important papers. These procedures could be used to adjust the parameters used in the decision rule to take into account differences in the measured scale features between the training samples and the fishery samples of unknown origin. The theoretical approach is simple. As the scale data from the individual fish comprising the fishery sample are classified these individuals are added to the training samples. For linear discriminant analysis the training sample means for each category and the pooled sample

TABLE 6. Classification array for the Horsefly, Late Stuart, Stellako, Birkenhead, and Weaver races.

Calculated decision	Correct decision Horsefly	Late Stuart	Stellako	Birkenhead	Weaver
Horsefly	42	14	11	24	22
Late Stuart	15	29	26	19	5
Stellako	7	22	22	17	11
Birkenhead	17	25	27	19	6
Weaver	22	12	12	13	67
Standard sample sizes	103	102	98	93	111

TABLE 7. Classification array for the Birkenhead, Weaver, Portage, and Lower Shuswap races.

Calculated decision	Correct decision Birkenhead	Weaver	Portage	Mara
Birkenhead	43	10	18	6
Weaver	12	59	23	9
Portage	14	21	34	10
Lower Shuswap	23	21	18	16
Standard sample sizes	93	111	93	41

TABLE 8. Classification array for the Birkenhead and Weaver races.

Calculated decision	Correct decision Birkenhead	Weaver
Birkenhead	71	19
Weaver	21	92
Standard sample sizes	92	111

TABLE 9. Overall classification accuracies for several combinations of stocks corresponding to anticipated in-season requirements.

Stock combination	Desired accuracy	Obtained accuracy
Lake Washington Early Stuart	75 %	100%
Lake Washington Early Stuart Nadina Horsefly Late Stuart	60 %	52%
Horsefly Late Stuart	75 %	69%
Horsefly Late Stuart Stellako Birkenhead Weaver	60 %	35%
Birkenhead Weaver Portage Lower Shuswap	62.5%	44%
Birkenhead Weaver	75 %	80%

variance–covariance matrix are updated to include the data from the current day's classification work. The updated parameters are then used to classify samples on the subsequent day. This process continues throughout the season. Theoretically the parameters soon shift to the "true" in-season values as the standards are "swamped" by the volume of fishery samples.

Practically, there are a tremendous number of problems with this approach, and it is unlikely that there would be any dramatic early successes. However, the feasibility of such an approach could be investigated along with a comprehensive study on scale pattern analysis without much additional effort. Unsupervised procedures are finding utility in other fields (Patrick 1972) and it would be worthwhile to determine the extent to which they might be applicable for Fraser River stock identification.

Summary

In this paper we have identified the requirements for in-season stock identification and the steps that the IPSFC has taken to address these needs. For the Fraser River these requirements are prodigious, and it will likely be several years before a complete system is implemented. The statistical approach for multiple stock complexes was addressed. The value of image processing for data acquisition was demonstrated with the prototype system; however, the desirability of systems with state of the art capabilities was indicated. Several problems remain. First, the issue of annual variability must be addressed with either unsupervised estimation or, perhaps, another methodology. Secondly, classification accuracy must be increased for certain stock complexes. This may not be possible where there is minimal scale pattern variability among stocks, but we feel that it is prudent to take advantage of the rapidly advancing image processing technology to further this goal. When these objectives are addressed, then it will be time to integrate the system within the management process with full consideration of the system's limitations and abilities. Accurate stock composition estimates would be utilized for in-season decision making while efforts continue to improve the results for inaccurate estimates.

Acknowledgements

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Section II
Fishery Management — Past, Present, and Future
b) Management of Some Principal Stocks

Sockeye Salmon (*Oncorhynchus nerka*) Management in Bristol Bay, Alaska

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Abstract

MINARD, R. E., AND C. P. MEACHAM. 1987. Sockeye salmon (*Oncorhynchus nerka*) management in Bristol Bay, Alaska. p. 336–342. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The Alaska Department of Fish and Game manages Bristol Bay sockeye salmon (*Oncorhynchus nerka*) on a maximum sustained yield basis. Annual harvest for the period 1976 through 1985 averaged 19 million sockeye salmon from total runs averaging 32.3 million. The primary management strategy is to regulate commercial fishing in five fishing districts to obtain an optimum spawning escapement in each of eight separate river systems. For systems where historic data exist, spawner-recruit analysis is used to establish the optimum number of spawners (escapement goal). Management ranges are set around the goal at values that would produce returns equal to 95% of the maximum yield achieved by the optimal point value and are therefore determined by each system's productivity pattern. Commercial catch is regulated by Commercial Fisheries Entry Commission limitations of numbers of fishermen, specifying fishing gear, restricting fishing areas, and limiting fishing times. A series of interrelated management and research projects is conducted at an annual operational cost of nearly $1 million to facilitate management of Bristol Bay salmon. Projects include: a pre-season forecast of adult returns; test fishing both offshore and within districts and rivers; catch tabulation and sampling; river escapement enumeration and sampling; and aerial surveys to assess numbers and distribution of fish. The resulting data are analyzed daily and used by local management biologists to set fishing time each day in each of the five commercial fishing districts.

Résumé

MINARD, R. E., AND C. P. MEACHAM. 1987. Sockeye salmon (*Oncorhynchus nerka*) management in Bristol Bay, Alaska. p. 336–342. *In* H. D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Le *ministère de la Pêche et de la Chasse* de l'Alaska gère le saumon nerka (*Oncorhynchus nerka*) de la baie Bristol sur la base du rendement maximal soutenu. Au cours de la période allant de 1976 à 1985, la récolte annuelle s'est élevée en moyenne à 19 millions de saumons nerkas pour des remontées totales moyennes de 32,3 millions de poissons. La grande stratégie de gestion appliquée consiste à réglementer la pêche commerciale dans cinq districts de pêche afin d'obtenir une remontée de frai optimale dans huit bassins versants distincts. On applique, aux bassins pour lesquels on dispose de données historiques, l'analyse par géniteurs-recrutement afin de déterminer le nombre optimal de géniteurs (objectif de remontée). Les gammes de gestion sont établies, en fonction de cet objectif, à des valeurs permettant d'obtenir une remontée égale à 95 % du rendement maximal obtenu à partir de la valeur optimale; elles sont donc fonction de la productivité de chacun des bassins. Les prises commerciales sont réglementées par la *Commercial Fisheries Entry Commission* qui détermine le nombre de pêcheurs, les engins, les zones et les périodes de pêche. Des travaux intégrés de gestion et de recherche dont les coûts d'opération annuels s'élèvent à près de 1 million de dollars sont réalisés afin de faciliter la gestion du saumon de la baie Bristol. On compte parmi ces travaux : une prévision d'avant-saison de la remontée des adultes, une pêche d'essai effectuée au large ainsi qu'à l'intérieur des districts de pêche et des cours d'eau, le traitement en tableaux des données de prise et d'échantillonnage, le dénombrement et l'échantillonnage des remontées en cours d'eau, de même que des relevés aériens visant à dénombrer et à déterminer la distribution des poissons. Les données obtenues sont analysées à chaque jour et utilisées par les biologistes locaux pour établir, à chaque jour, les durées de pêche dans chacun des cinq districts de la pêche commerciale.

Introduction

Although Bristol Bay includes a relatively large geographic area (Fig. 1), commercial fishing is limited to five major fishing districts which include Bristol Bay's eight primary river systems. These districts support commercial harvests of five species of Pacific salmon (*Oncorhynchus* sp.).

Bristol Bay produces the largest sockeye salmon runs in the world. Commercial sockeye harvests began in 1893 and have averaged 11.8 million fish annually through 1985. Since its inception this fishery has harvested a total of 1.1 billion sockeye salmon. As illustrated in Fig. 2, the fishery developed rapidly and by 1913 the annual harvest exceeded 20 million sockeye. A sustained period of high harvests continued through 1938, during which annual harvests averaged over sixteen million sockeye. From 1939 to 1974, the catch declined, averaging only eight million sockeye per year. From 1979 to 1985, commercial harvests have been at an all-time high, averaging nearly 25 million sockeye salmon per year. During the 1978–82 years, Bristol Bay contributed 68% of the Alaskan, 63% of the U.S., and 46% of the Pacific Rim sockeye salmon production. Value of the sockeye fishery has ranged from 2.7 to 122 million dollars shared by 4 554 participating fishermen. Both 150 fathom drift gill nets fished from 32 foot gill net boats and 50 fathom set gill nets attached to the beach are considered legal fishing gear.

Before inception of the commercial fishery there was a subsistence harvest by Native Alaskans. Even today subsistence salmon fishing is significant in both numbers of fish utilized as well as its cultural importance to watershed residents. Subsistence harvests have averaged 144 000 (range 93 000–213 000) fish per year from 1963–1985. Subsistence fishing is granted the highest allocative priority between user groups.

After spending usually two to three years in fresh water, Bristol Bay sockeye salmon migrate to sea and return as primarily 4-, 5-, and 6- yr-old fish. While at sea, sockeye follow an elliptical migration path that extends westerly toward the Kamchatka Peninsula of the Soviet Union then easterly to the Gulf of Alaska (Straty 1975). The onshore movement toward natal streams commences in early May with stocks moving directly toward southerly passes of the Aleutian Islands from the feeding grounds in the Gulf of Alaska. Migrational paths then take a general northeasterly course up the Alaska Peninsula towards Bristol Bay.

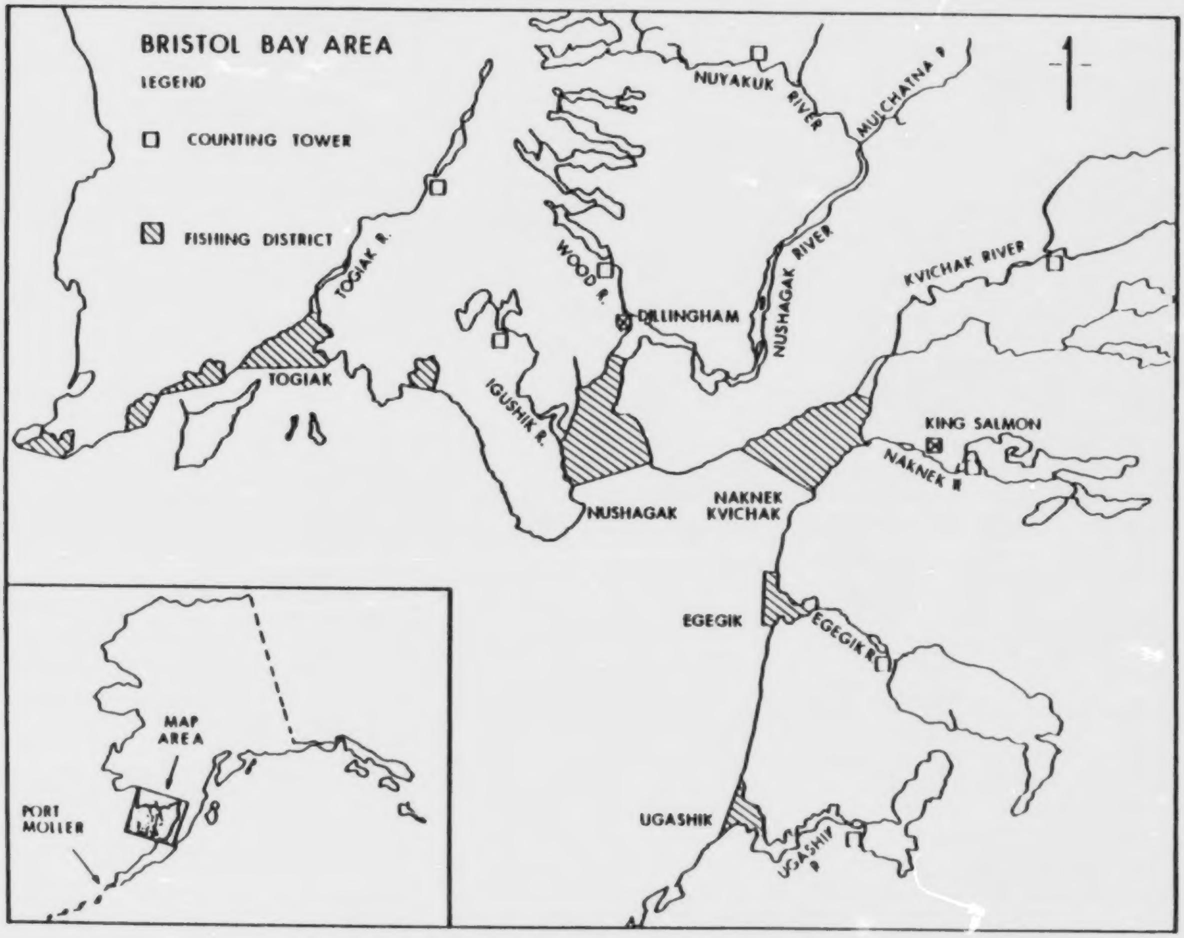

FIG. 1. Bristol Bay and associated commercial fishing districts.

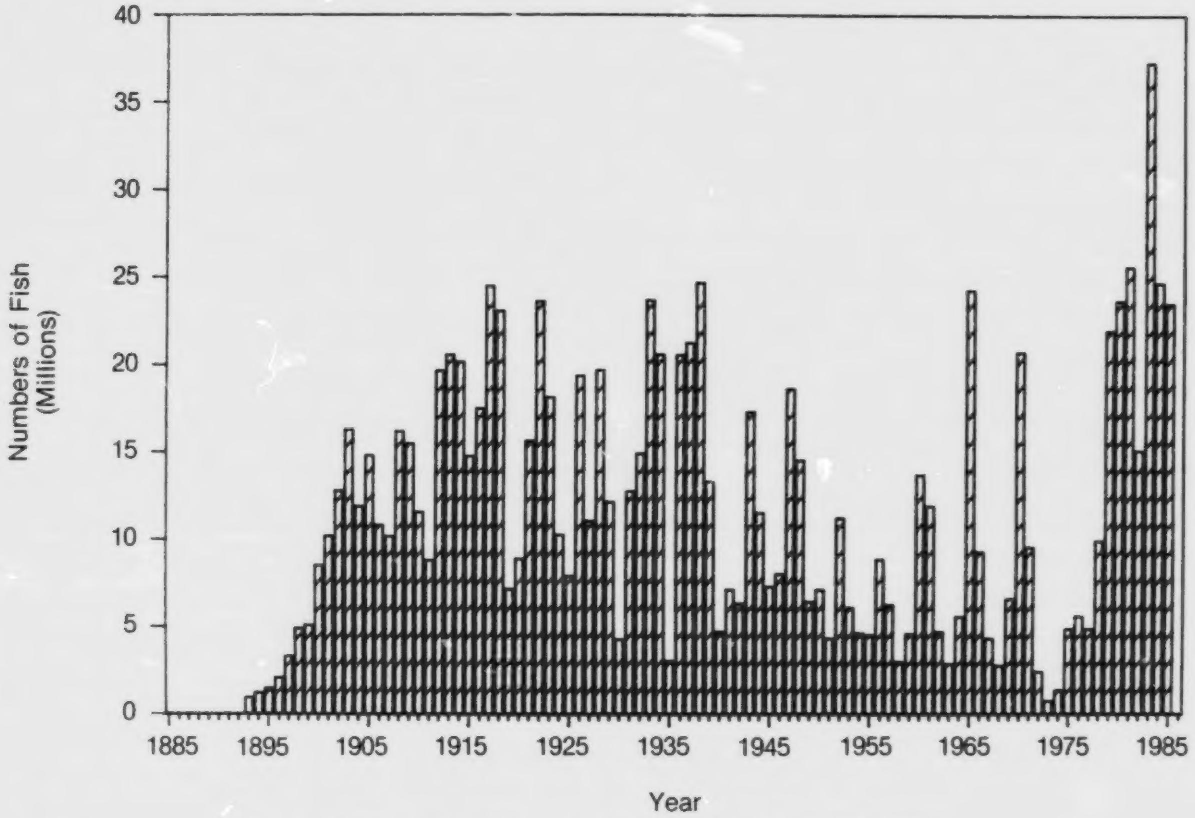

FIG. 2. Commercial harvest of sockeye salmon in Bristol Bay, 1893–1985.

Although the commercial fishery in Bristol Bay extends from late May into September, the sockeye salmon fishery is very concentrated with about 65% of the run passing through the fishing districts in a two week period. Run timing is relatively consistent among years with peak abundance occurring around July 4th. Because of this concentration, specialized real time management techniques have been developed to gauge and control the rate of exploitation to allow achievement of preset escapement goals. The purpose of this paper is to present an overview of Bristol Bay sockeye salmon management by reviewing the objectives and practices currently utilized by the Alaska Department of Fish and Game.

Management Goals and Objectives

The primary management strategy is to regulate commercial fishing by openings and closures in five fishing districts to obtain optimal numbers of spawners in each of eight major river systems. Concurrent with this strategy, management is directed by essentially three goals: manage for maximum sustained yield (MSY), provide for an orderly harvest of stock surpluses, and ensure product quality. Managing stocks for MSY, of foremost importance to the fishery manager, is realized through terminal fisheries establishment of river specific escapement goals, and preserving genetic diversity by distributing catches and escapements over the entire run.

Fundamental to the basic strategy is the concept of terminal or discrete stock fisheries management. Each of the river specific stocks returning to Bristol Bay is managed, to the extent possible, as an individual entity. Commercial fishing openings and closures are predicated on attainment of escapement goals and are implemented by flexible rather than fixed fishing schedules. Authority to open and close fishing districts by emergency order has been delegated to biologists located near the fishing grounds, allowing rapid management response time. Each of the five districts is thereby managed independently to conform to the individual stock characteristics of run timing and strength.

Spawner-recruit (Ricker 1954) analysis is used to establish optimum numbers of spawners for each major river system. Optimal escapement is defined as the point on the spawner recruit curve where surplus production is maximized. While fishery management decisions are directed toward achieving the optimum escapement an acceptable management range is also calculated. Management ranges placed around escapement goals are set at 95% of the maximum yield achieved by the optimal point value and are therefore determined by each system's individual productivity as defined by the shape of the spawner-recruit curve. A broad spawner-recruit curve suggests a system will produce nearly equally over a wide range of escapements, whereas a narrow spawner-recruit curve suggests a system will produce best over a relatively narrow range of escapement.

Management Infrastructure

Although simple in concept, the achievement of management objectives is exceedingly complex. Each day a complicated series of programmatic analyses are run concurrently which provide in-season assessments of run timing, magnitude, age composition, catch and escapement levels, as well as a multitude of additional inputs. Approximately 30 management and research projects provide input over a 10 month time span commencing with the pre-season forecast of adult returns in December and continuing to the end of the fishing season in late August. Singly these projects give only limited insight, but pooled, they form a relatively complete synopsis of run size.

The first estimate of the strength of adult returns is from pre-season forecasts formulated as early as 10 months in advance. Forecasts by returning age class and river system are generated by four methods (Fried 1985), using smolt data, sibling returns, spawner recruit analysis, and lastly, high seas gillnet CPUE data. The individual forecasts are combined after being weighted by the inverse of their relative standard error (determined by past performance) in order to generate a composite Bristol Bay forecast. With an average error of 36%, the composite forecast is an integral part of preseason planning for sockeye salmon runs that have ranged from 2 to 65 million since 1973. Managers utilize the forecasts primarily to develop management strategies for the coming season. Fishing industry representatives base preseason marketing and processing plans on potential harvest estimated by subtracting numbers in escapement goals from numbers forecasted. Fishermen use forecasts of age composition when selecting gillnet mesh size and deciding which district(s) to fish.

The forecast of Bristol Bay sockeye salmon is also used to establish a catch quota in the Shumagin Island and South Unimak interception fisheries located 500 miles to the southwest. In early June as the migrating sockeye move towards passes in the Aleutian Islands, management staff closely watch the catches made in these interception fisheries. Although local stocks exist in this area, extensive tagging data (Thornsteinson and Merrell 1964) indicate that the catch is primarily from North Peninsula and Bristol Bay stocks. Catch per unit effort (CPUE) information, along with a recently developed catch sampling program provide run timing, magnitude relative to past years, and age composition data approximately 12–14 days in advance of the fish arriving in Bristol Bay. Data are used subjectively because statistical analysis has failed to prove a predictable link between CPUE in these districts and absolute sockeye abundance observed in Bristol Bay.

The first quantitative evaluation of pre-season forecasts come from a test fishery conducted offshore of Port Moller on the north side of the Alaskan Peninsula. Offshore test fishing, conducted since 1967, has been used to predict total sockeye salmon run size about 6 to 7 days prior to their arrival at inshore commercial fishing districts within Bristol Bay (Randall 1977; Meacham 1979; Huttunen 1980, 1982; Eggers 1984). Gill netting is conducted at 11 stations, on about 8 km (5 mi) intervals along a transect extending northwesterly from Port Moller. Drift gill nets of 364 m (200 fm) are used and catches are expressed as indices in terms of salmon caught/180 m (100 fm) × h^{-1}. Indices provide estimates of daily and cumulative sockeye passage. Data from scale samples collected from test fishery catches are combined with indices which then provide abundance estimates by age class. Projections of total run size are made by dividing estimated cumulative sockeye passage by the expected cumulative proportion for a given date. A statistically significant correlation was found between average length and weight of fish and total run size and this is used to provide an estimate of total abundance (Fried 1985). More recently temperature data have been included in the regression and this improved accuracy of the estimates.

Within-district commercial CPUE and within-district test fishing operations yield the next assessment of run timing, age composition, and relative size. Early commercial fishing openings are often used to judge run strength within a given district. Commercial processors are required to provide oral catch reports to the Department immediately after each commercial fishing period, or daily during periods of extended fishing. Oral catch reports are confirmed through a mandatory fish ticket system that requires buyers to complete a fish ticket for each landing, identifying catch, location, date, vessel, and fisherman. Intensive catch sampling is also conducted at processing sites after each commercial fishing period. Each year approximately 10 000 samples of scales, sex, length, and weight data are routinely collected. Age summaries are provided to management staff often within hours of collection. District catches alone are not sufficiently accurate measures of abundance, but when coupled with age composition and historical timing, they help to identify age class strengths and failures relative to pre-season forecasts and offshore test fishing at Port Moller.

Migrating fish which have escaped the commercial fishery move into the muddy lower reaches of the major river systems and are indexed by in-river test fishing projects using drift, or set gill nets. Index values are calculated in the same manner as those for the Port Moller test fish project. Escapement estimates are then made by multiplying accumulated test fishing index values by an escapement per-index point multiplier derived by two procedures. The first is based on past year's results (dividing the total counted escapement by the total number of index points generated for a season), and adjusted for gillnet effectiveness based on the size of the fish. The second method, used later in the season after some fraction of the actual escapement has been enumerated, provides a multiplier derived by dividing the escapement to date by the cumulative test fish indices lagged back a sufficient number of days to account for travel time between the test fishery and counting station. Lag times are determined by tagging and by comparing entry patterns detected by the test fishery and at the counting tower. Inriver test fish projects provide the first quantitative measure of escapement by river system.

Low level fixed wing aerial surveys of migrating fish help to validate test fishing indices but are limited to those portions of rivers where visibility is sufficient to allow observers to actually distinguish fish. Aerial surveys provide an intermediate count prior to the final escapement estimates collected at counting stations located on the eight major sockeye producing systems in Bristol Bay. At these stations fisheries technicians visually count spawners as they migrate past wooden or aluminum scaffold counting towers erected at the river's edge. Counts of 10 min duration on each side of the

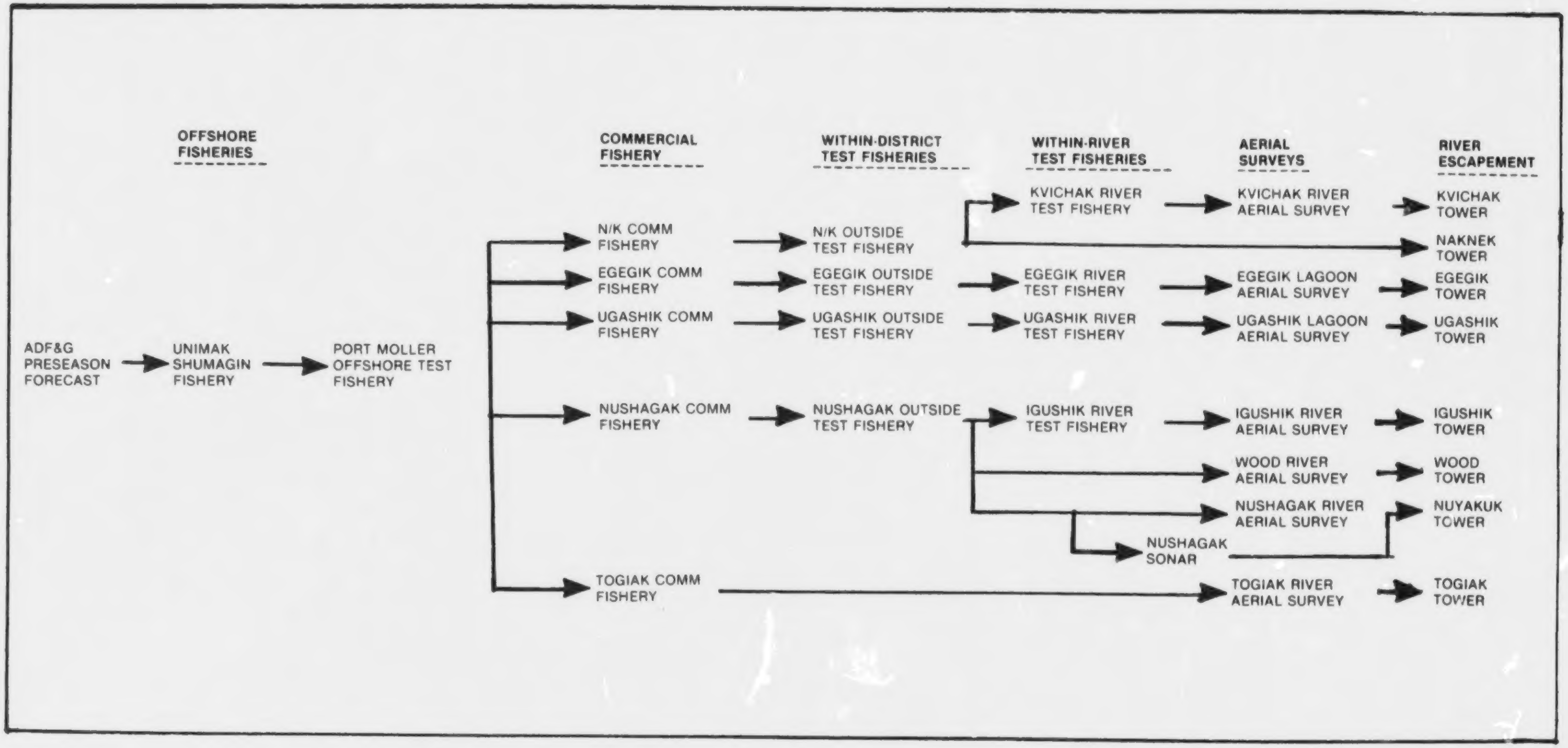
OFFSHORE FISHERIES
COMMERCIAL FISHERY
WITHIN-DISTRICT TEST FISHERIES
WITHIN-RIVER TEST FISHERIES
AERIAL SURVEYS
RIVER ESCAPEMENT
ADF&G PRESEASON FORECAST
UNIMAK SHUMAGIN FISHERY
PORT MOLLER OFFSHORE TEST FISHERY
N/K COMM FISHERY
EGEGIK COMM FISHERY
UGASHIK COMM FISHERY
NUSHAGAK COMM FISHERY
TOGIAK COMM FISHERY
N/K OUTSIDE TEST FISHERY
EGEGIK OUTSIDE TEST FISHERY
UGASHIK OUTSIDE TEST FISHERY
NUSHAGAK OUTSIDE TEST FISHERY
KVICHAK RIVER TEST FISHERY
EGEGIK RIVER TEST FISHERY
UGASHIK RIVER TEST FISHERY
IGUSHIK RIVER TEST FISHERY
NUSHAGAK SONAR
KVICHAK RIVER AERIAL SURVEY
EGEGIK LAGOON AERIAL SURVEY
UGASHIK LAGOON AERIAL SURVEY
IGUSHIK RIVER AERIAL SURVEY
WOOD RIVER AERIAL SURVEY
NUSHAGAK RIVER AERIAL SURVEY
TOGIAK RIVER AERIAL SURVEY
KVICHAK TOWER
NAKNEK TOWER
EGEGIK TOWER
UGASHIK TOWER
IGUSHIK TOWER
WOOD TOWER
NUYAKUK TOWER
TOGIAK TOWER

FIG 3. Diagramatic representation of Bristol Bay management and research activities.

river, each hour, are expanded to estimate total escapement in each 24-h period. It is these estimates that are considered final estimates of escapement. During the peak of the season, escapement counts are radioed to management biologists at 4-h intervals throughout the day. These final estimates are ultimately the gauge by which management success is measured. However, counting towers are generally many miles upstream so escapement estimates may lag behind the active fishery by as much as 2 wk. This delay often reduces their utility for in-season management decisions, thus necessitating the aforementioned intermediate counts (in-river test fishery and aerial survey). Biological sampling of the escapement is conducted at each tower, providing a total escapement sample of 15 000 age, length, and sex samples each year.

On the Nushagak River the intermediate escapement assessment tools have been replaced with a Bendix side scan sonar system that is located 35 miles upstream of the commercial fishing district boundary. This hydroacoustic system records fish passage continuously throughout the run. Samples of migrating fish are seined daily to determine species composition, and sonar counts are apportioned by species accordingly. This process provides management staff relatively accurate daily escapement estimates shortly after the fish have escaped the fishery and considerably earlier than can be obtained at the counting tower (Minard 1984).

This process begins with the preseason forecast and ends with final catch and escapement counts by river system (Fig. 3). Intermediate projects sequentially provide assessments of abundance that improve in accuracy as individual stocks separate and enter natal streams.

Decision-Making Process

The primary objective of Bristol Bay sockeye salmon management is to achieve escapement goals specified for each of eight major rivers. The first step taken towards achieving this objective is to restrict fishing to five separated commercial fishing districts surrounding individual or adjacent river mouths and disallow fishing in areas between districts. The resulting relatively discrete stock fisheries allow exploitation rates to be adjusted to match stock strength by river. The second step is to monitor numerical stock strength and fishing effort. This is accomplished through over thirty individual projects operated during June and July. The daily volume of data, the sophisticated analytic evaluation required, and the need for real time inputs to the management decision making process require computer application (Yuen 1980).

Every morning a small team of management and research biologists reviews the most recent information and considers pertinent analytic interpretations. It is at these meetings that fishing decisions or options for later action are established. The management biologists are empowered to issue emergency orders opening the fishery, while research biologist are responsible for operation and interpretation of a number of field projects providing information critical to the decision making process. This organizational structure promotes discussion between biologists and generally results in a well thought out but timely decision.

All management decisions are documented through the written "emergency order" process and in a management report written each year. Emergency orders are formal documents, generally a page or two in length, which contain a simplified explanation of the management decision, the specific regulatory action in legal terms, and a justification for the decision that was made. They are signed by the management biologist on the scene of the fishery through authority previously granted in writing by the Commissioner of the Department of Fish and Game. All field projects are also documented, either in the Alaska Department of Fish and Game Informational Leaflet series or the Technical Data Report series. Documentation of data and management decisions have been a high priority of the salmon management program in Bristol Bay, allowing wide dissemination of project and management information with resulting program improvements. This has also facilitated a smooth transition during changes in management personnel.

In addition to the largely analytical field projects designed to monitor stock strength and fishing effort by district as described previously, there are a number of more subjective considerations called upon to assist in the management process. Chief among these is the assessment of mixed stocks within a single commercial fishing district as occurs annually in the Nushagak and Naknek-Kvichak districts. In each of these districts adjacent rivers contribute sockeye salmon to a common commercial fishery. Decisions must be made to either exceed or fall short of the escapement goal for each river since generally only a single exploitation rate is possible for a given fishing district but each contributing river's stock requires a unique exploitation rate in order to catch the harverstable surplus above escapement needs. For example, in the Nushagak district salmon returns to the Wood River would dictate an exploitation rate of 0.5 while returns to the adjacent Nushagak River would require an exploitation rate of 0.3. In order to harvest fully Wood River fish, Nushagak River fish would be overharvested with subsequent failure to meet Nushagak River escapement objectives. Management decisions are made even more difficult by the presence of mixed species. Management decisions have been made to harvest an abundance of chum salmon at the expense of achieving sockeye salmon escapements. At the present time, management decisions dealing with mixed stock and mixed species are rather subjective.

The sockeye salmon escapement of the preceeding year or, less commonly, the anticipated following year run strength occasionally influences management decisions. Management biologists tend to take greater risks and be more liberal with fishing time if, during the prior year or two, a given river has received escapements somewhat above the escapement goal. Conversely, if a river has not achieved its escapement goal during the past year or two, a management biologist may take a more conservative posture which results in slightly exceeding the escapement goal. In both instances the management biologist considers a multi-year surplus or deficit of spawners relative to the degree of risk associated with a fishing decision.

To improve the Bristol Bay management system greater attention should be given to methods for quantifying these subjective considerations, e.g., for determining the value of an escaping sockeye salmon in one river relative to one caught from another river. Similar relative value judgements are needed between sockeye and other salmon species. Different prices paid per pound, different levels of productivity between species, and different productivity levels for a given species at various escapement levels will require considerable time and analytic effort to optimize production.

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The Cycle of Runs of Sockeye Salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: Cyclic Dominance or Depensatory Fishing?

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Abstract

EGGERS, D. M., AND D. E. ROGERS. 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: cyclic dominance or depensatory fishing?, p. 343–366. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The study examined two competing hypotheses seeking to explain the Kvichak cycle: (1) existence of a depensatory agent independent of the fishery and (2) depensatory fishing. The first hypothesis was implicit in the status quo harvest policy. Available data were analyzed to evaluate the alternative hypotheses. Little evidence for direct depensatory mortality independent of the fishery was found, however, production was depressed in brood years following large escapement brood years. In addition, the fishery itself was found to be extremely depensatory. A stochastic empirical computer simulation model incorporating processes found in the data analyses, was used to examine the consistency of brood year interaction with the depensatory fishing hypothesis and historical cyclic patterns in the Kvichak run. The model predicted weak cyclic patterns in the unexploited run and strong cyclic patterns, consistent with the historical pattern, in the run exploited under the status quo harvest policy of cyclic escapement goals. The model was then used to evaluate alternative harvest policies. There were almost no differences in simulated catches under the status quo and static fixed escapement goal and static rate of exploitation policies. Substantial increases in simulated catch occurred with a dynamic policy of alternate years of high escapements following years of low escapement. This harvest policy can be phased with the cycle of resulting runs based on a forecast of future runs. The study suggested that the present Kvichak sockeye management policy should be altered by reducing the prepeak escapement goal and establishing a second peak cycle run.

Résumé

EGGERS, D. M., AND D. E. ROGERS. 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: cyclic dominance or depensatory fishing?, p. 343–366. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les auteurs ont étudié deux hypothèses concurrentes visant à expliquer le cycle des remontées dans la rivière Kvichak : 1) l'existence d'un facteur anticompensatoire indépendant de la pêche et 2) une pêche anticompensatoire. La première hypothèse est implicite dans la politique de récolte du statu quo. Les données disponibles ont été analysées afin d'évaluer les deux hypothèses. On a trouvé peu de faits indiquant une mortalité anticompensatoire directe indépendante de la pêche, mais la production était plus faible au cours des années de reproduction faisant suite aux années d'importantes remontées. De plus, la pêche s'est avérée être extrêmement anticompensatoire. Un modèle de simulation informatique empirique et stochastique des processus notés au cours de l'analyse des données a servi à étudier la cohérence de l'interaction entre les années de reproduction et l'hypothèse de la pêche anticompensatoire et le régime historique cyclique des remontées dans la Kvichak. Le modèle prévoyait un régime cyclique faible pour les remontées non exploitées et un régime cyclique fort, conforme à l'allure historique, pour les remontées exploitées conformément à la politique de récolte du statu quo basée sur des échappés cycliques. Le modèle a ensuite été utilisé pour évaluer d'autres politiques de récolte. Il n'y avait pratiquement aucune différence entre les valeurs des prises simulées obtenues par la politique du statu quo et celle de l'objectif statique fixe des remontées, et celles des politiques d'exploitation à taux statique. Des augmentations appréciables des prises simulées ont cependant été notées dans le cas de l'application d'une politique de récolte dynamique où l'on faisait alterner des années de remontées importantes avec des années de faibles remontées. Cette politique de récolte pourrait être appliquée en phase avec le cycle des remontées obtenues, sur la base des prévisions des remontées à venir. L'étude porte à croire que la politique de gestion actuelle du saumon nerka de la Kvichak pourrait être modifiée en réduisant l'objectif des échappées d'avant pic et en établissant un deuxième pic de remontées cycliques.

Introduction

This study attempts to evaluate two contrasting hypotheses for explaining the cycle of runs of sockeye salmon, *Oncorhynchus nerka* (Walbaum), to the Kvichak River system, Bristol Bay, Alaska. The two competing hypotheses, which have vastly different management implications, are cyclic dominance and depensatory fishing.

The Kvichak River system (Fig. 1) is the largest producer of sockeye salmon in Alaska. The annual run to the Kvichak is also one of the most variable in Alaska, ranging from 300 thousand to 42 million, since 1950. Kvichak sockeye are exploited in the Bristol Bay sockeye salmon fishery, particularly in the Naknek-Kvichak district along with the usually less abundant and less variable stocks from the Branch and Naknek River Systems (Fig. 1), (see Mathisen 1979; Minard and Meacham 1987, for a description of the current fishery and management system).

The present Bristol Bay fishery began with the construction of a saltery in 1883, 15 years after Alaska was purchased from the Russians in 1867 (Mathisen 1979). Prior to 1883, salmon were harvested in Bristol Bay by Native food or subsistence fisheries. The historical annual Alaska-wide subsistence catch by these native fisheries is thought to be in excess of 10 million fish (Pennoyer 1979). These aboriginal subsistence fisheries were substantial, being roughly 10% of the recent Alaska catch of salmon now at maximum historical levels (Eggers 1985).

Prior to 1924, Bristol Bay fisheries regulations consisted of keeping the fleet below the intertidal zone and reducing its efficiency. Powerboats were banned in 1923 and gill net mesh size was restricted (14.61 cm 1913–26, 13.97 cm 1927–60). The earlier mesh sizes were less effective than the present ones of 13.65 cm. The White Act of 1924 sought to divide evenly each river's catch and escapement, but this was never achieved. Fish counting weirs were erected on some rivers as a means of assessment but they proved costly and inefficient. Consequently, escapement magnitudes were poorly accounted for and management was often ineffective because of remote (Washington, D. C.) regulatory control. The early Bristol Bay fishery was essentially a quota fishery, being limited by canning capacity (Mathisen 1979).

During the late 1940's, reacting to declining Alaskan runs, the Alaska Salmon Canning Industry commissioned Dr. W. F. Thompson, the first director of the Fisheries Research Institute (FRI) at the University of Washington, to organize life history studies of sockeye salmon in Bristol Bay. The more cost-effective monitoring techniques developed in these studies coupled with Alaska statehood and the eventual esta-

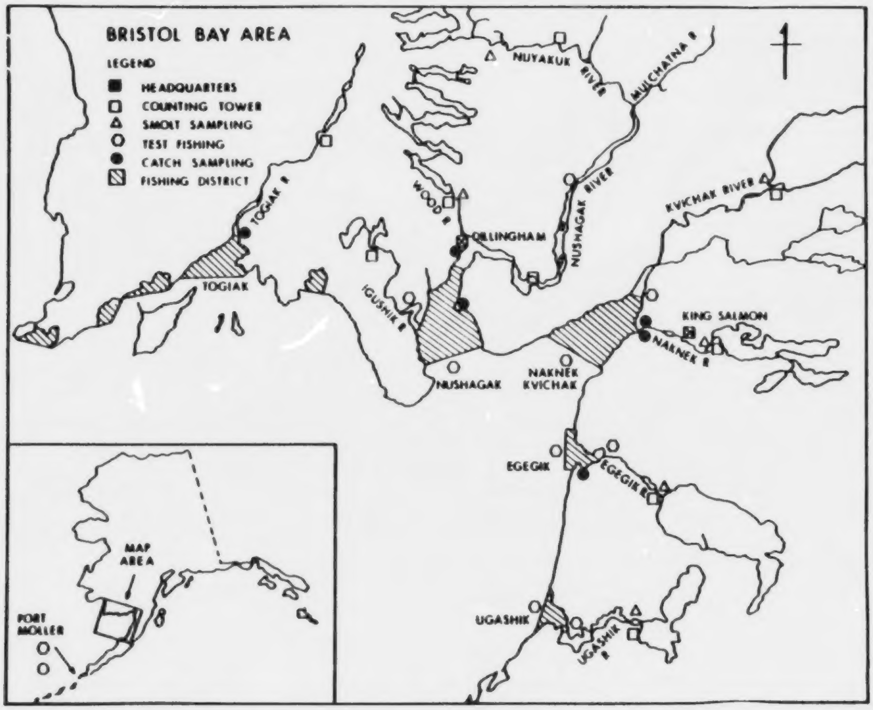

FIG. 1. Bristol Bay sockeye salmon river systems, fishing districts, and sampling programs of the Bristol Bay management system.

blishment of local regulatory control, culminated in the implementation by the State of Alaska of real time fishery management to achieve escapement goals by river system (Mathisen 1979: Minard and Meacham 1987).

After buildup of the fishery in the early 1900's and until the mid-1930's, the Naknek-Kvichak stocks produced about three consecutive large catches out of every five years (Mathisen and Poe 1981; Rogers and Poe 1984). From then until the mid 1940's the stocks have produced two consecutive large catches in every five years. During the period covering the 1952-78 brood years, the Kvichak River system has produced only one large return in 4 or 5 yr (Fig. 2). The autocorrelation function (Nisbet and Gurney 1982) for the time series of Kvichak runs from 1956 to the present show a cyclic pattern with a 5-yr periodicity (Fig. 2). More recently the pattern of runs to the Kvichak has been similar to that of 1900-40 as inferred from the catches of that period. For instance, large runs of 20, 23, and 14 million fish occurred in 3 consecutive years beginning in 1983.

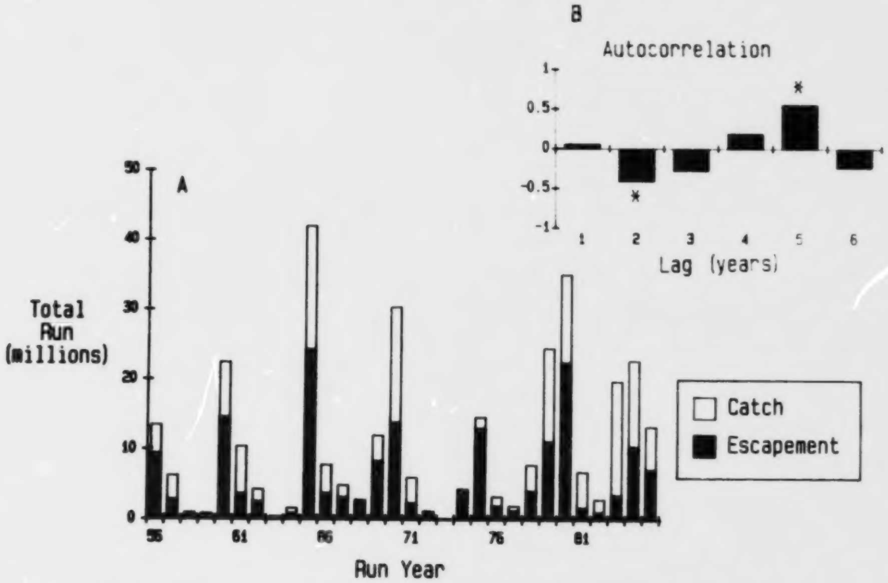

FIG. 2. (A) Total inshore run (catch + escapement) of sockeye salmon to the Kvichak River, 1956-85. (B) Estimated autocorrelation coefficient (asterisks indicate significance ($P<0.05$) for the time series of Kvichak return in A).

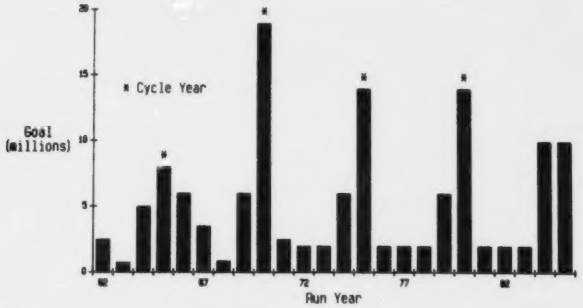

FIG. 3. Target escapement goals for Kvichak River sockeye salmon, 1962-85. Asterisks indicate peak cycle run years.

The Kvichak stock has been managed since the 1960's based on a cyclic escapement goal (Fig. 3). Here the strategy has been to obtain a large escapement (10-15 million) for the peak cycle run, an intermediate escapement (4-6 million) for the pre-cycle year, and small escapements (1-2 million) for the other years (Fig. 2). The strategy for other Bristol Bay River systems has been to manage to the same fixed escapement goal every year.

The rationale for the cyclic escapement strategy for the Kvichak stock was based on the theory of cyclic dominance (Ricker 1950, 1962; Ward and Larkin 1964; Larkin 1971; Mathisen and Poe 1981). A necessary condition for cyclic dominance is to have a stock with a single age at maturity or a tendency to return at a single age at maturity. The former is true for pink salmon and the latter is true for certain sockeye salmon stocks, including the Kvichak River system and upriver stocks of the Fraser River system. Briefly, under the cyclic dominance hypothesis there exists a depensatory (cf. Ricker 1954; Larkin et al. 1964) agent or agents independent of the fishery which suppresses the production from small escapements. Because cycles of runs have not been in phase among pink salmon stocks that utilize common marine rearing areas, or among the cyclic stocks within the Fraser River, the depensation has been thought to occur in fresh water (Ricker 1950, 1962). Several agents or mechanisms have been proposed but the most widely held view is that the Fraser River cyclic dominance is caused by depensatory lacustrine predation and perhaps an interaction between the peak-cycle and post-cycle years (Ward and Larkin 1964). The cycle year interaction is thought to be either direct competition, and/or depensatory effects of the delayed predator response to the disappearance of the cycle year smolt from the lake moderated by the buffering of depensatory predation when progeny from cycle and post-cycle brood years co-occur in the lake (Ward and Larkin 1964). Cycles may be further reinforced by lacustrine fertilization by salmon carcasses (Donaldson 1967), which may mitigate the adverse effects of density dependent growth and thus help maintain cycles. Note that fertilization by itself is not a depensatory effect, and therefore cannot initiate cycles.

Under the cyclic dominance hypothesis, cycles would occur in unexploited populations, and further, any deliberate management for non-cyclic returns would be counterproductive. Overharvesting the cycle return would lead to catastrophic declines. The disastrous effect of the Hell's Gate obstruction on subsequent year returns of sockeye salmon to the Fraser (Thompson 1945) has been widely cited in support of this.

Recent unanticipated changes in the Kvichak cycle described above, have prompted a re-evaluation of the concept that the Kvichak cycle is maintained by cyclic dominance. These changes were precipitated by: (1) The very high production that was observed for the pre-cycle year 1974, in which the escapement (4.4 million) was far less than cycle year levels; (2) Large escapements were achieved in two consecutive years, 1979 and 1980. These resulted from excellent production observed for the 1974 and 1975 brood years, as well as reduced fishing effort in both years due to a price dispute between fishermen and processors; (3) There was a change in the historical pattern in which there was a tendency for large escapements to the Kvichak to produce returns that were predominantly one age at maturity; (4) There has been a change in the distribution of spawning within the Kvichak River system since 1974, with increased utilization of the Lake Clark spawning areas and decreased utilization of the Island Beaches spawning areas (Rogers and Poe 1984).

The biological aspects of these changes have been shown to be density independent, and therefore inconsistent with the cyclic dominance hypothesis (Rogers and Poe 1984). The excellent production observed for the 1974 and 1975 brood years was coincident with phenomenal increases in salmon production observed throughout Western and Central Alaska (cf. Rogers 1984), and is thought to be due to a combination of favorable environmental conditions in the North Pacific and Bering Sea, as well as reduced interception by high seas fisheries (Rogers 1984; Eggers et al. 1984). The changes in age at maturity were due to warm weather during the period of lacustrine residence of the 1979 and 1980 brood years (Rogers and Poe 1984; Rogers 1984).

These events and their inconsistency with the cyclic dominance hypothesis have prompted consideration of an alternative hypothesis explaining the cyclic returns of sockeye to the Kvichak. It is that the fishery is the depensatory agent that has caused and maintained the cycle.

The management implications of the depensatory fishing hypothesis are quite different from those of the cyclic dominance hypothesis. Cyclic returns represent problems for the industry. Prices are depressed in cycle years and there are high costs associated with maintenance of processing and harvesting capacity that is idle during off-cycle years. If the capacity of the Kvichak River system to produce salmon is reflected in the cycle year production then a management policy of cyclic escapement goals represents a policy of extreme overfishing. If the depensatory fishing hypothesis is correct, then large gains in both production as well as economic efficiency can be expected by increasing escapements in the off-cycle years.

The management required under the two alternative hypotheses during off-cycle years are completely different. Because of this a careful evaluation of the two hypotheses is warranted before management objectives are changed. This was the motivation of our evaluation.

APPROACH

The study consisted of four components: evaluation of depensation, model identification, model evaluation, and harvest policy evaluation. In the evaluation of depensation phase of the study we examined the existence and relative importance of non-fishery and fishery related depensatory mortality. We were looking specifically for a depensatory agent in the lacustrine phase of the Kvichak sockeye life history. The second component of the study (Model Identification) was to construct a stochastic simulation model incorporating any depensatory or non-depensatory tendencies in the data as identified in the evaluation of depensation phase of the study. The approach was to identify empirical processes by fitted deterministic relationships together with estimated probability distributions for associated residuals. These individual processes were synthesized in a computer model that simulated the long-term return expected under alternative harvest policies. In the model evaluation phase of the study, we examined the model's ability, with the status quo policy of cyclic escapement goals implicit, to recapitulate: (1) historical cyclic patterns and magnitudes of run (i.e., catch plus escapement); (2) the observed frequency distributions of freshwater and marine age at maturity, together with return, escapement, and return per spawner. In the fourth component of the study (Harvest Policy Evaluation) the model was used to evaluate alternative management policies with respect to expected yield to the fishery.

Evaluation of Depensation

Rogers and Poe (1984) reviewed historical changes in the Kvichak sockeye cycle. The type and sources of data reviewed in the study are as follows: (1) Pre-1952 Naknek-Kvichak district catches by age and brood year collected by the Bureau of Commercial Fisheries (BCF) and summarized by Mathisen (1964); (2) Post-1952 data from catches and escapements (Table 1) including length, weight, sex, and age composition statistics collected by BCF, FRI, and Alaska Department of Fish and Game (ADFG) and summarized in ADFG reports (see Yuen et al. 1986, which is the latest in the series, for citations of earlier reports). Catches were determined from receipts for fish delivered to processors, escapements were determined by visual counts from towers erected on river banks, and catches were allocated to individual river systems based on relative escapement magnitudes by age class. Note that Rogers and Poe (1984) used inshore returns and the following analyses uses inshore returns plus high seas catches prorated to individual river systems according to the relative contributions of the respective river systems to the inshore Bristol Bay run; (3) Annual estimates of abundance, age composition, and size (i.e., length and weight) of outmigrating sockeye smolts from the Kvichak River collected

TABLE 1. Escapement and return (thousands) by age-group for Kvichak River sockeye, 1956–80 brood years. Returns include estimates of Kvichak sockeye intercepted in high seas fisheries.

Year	Escapement	Return by Age-Group										Total	R/S
		1.2		1.3		2.2		2.3		Other			
		#	%	#	%	#	%	#	%	#	%		
1956	9 443	24 185	62.4%	6 887	17.8%	6 397	16.5%	1 272	3.3%	14	0.0%	38 755	4.10
1957	2 843	240	6.0%	238	6.0%	3 238	81.3%	254	6.4%	12	0.3%	3 982	1.40
1958	535	74	26.3%	47	16.7%	132	46.9%	25	8.9%	4	1.3%	282	0.53
1959	680	208	38.9%	114	21.3%	202	37.7%	10	1.9%	1	0.2%	535	0.79
1960	14 630	1 285	2.4%	556	1.0%	46 139	84.8%	6 296	11.6%	148	0.3%	54 424	3.72
1961	3 706	329	9.7%	184	5.4%	2 225	65.3%	664	19.5%	6	0.2%	3 408	0.92
1962	2 581	101	1.9%	148	2.8%	4 568	87.6%	383	7.3%	17	0.3%	5 217	2.02
1963	339	47	4.6%	47	4.6%	600	58.4%	318	31.0%	15	1.5%	1 027	3.03
1964	957	2 096	38.2%	351	6.4%	2 295	41.9%	624	11.4%	115	2.1%	5 481	5.73
1965	24 326	9 640	22.1%	451	1.0%	31 729	72.9%	1 213	2.8%	510	1.2%	43 543	1.79
1966	3 775	478	7.9%	1 056	17.4%	4 129	68.2%	360	5.9%	31	0.5%	6 054	1.60
1967	3 216	319	22.6%	254	18.0%	748	53.1%	81	5.7%	7	0.5%	1 409	0.44
1968	2 557	270	52.5%	31	6.0%	75	14.6%	131	25.5%	7	1.4%	514	0.20
1969	8 394	123	2.3%	320	6.1%	4 199	79.7%	589	11.2%	37	0.7%	5 268	0.63
1970	13 935	43	0.3%	12	0.1%	14 323	91.4%	829	5.3%	456	2.9%	15 663	1.12
1971	2 387	242	8.7%	91	3.3%	2 117	76.5%	296	10.7%	20	0.7%	2 766	1.16
1972	1 010	249	13.1%	156	8.2%	1 178	62.1%	290	15.3%	23	1.2%	1 896	1.88
1973	227	563	23.4%	1 004	41.7%	267	11.1%	535	22.2%	37	1.5%	2 406	10.60
1974	4 434	6 177	24.1%	1 981	7.7%	16 383	63.9%	744	2.9%	346	1.4%	25 631	5.78
1975	13 140	5 523	15.4%	1 212	3.4%	28 261	78.8%	563	1.6%	306	0.9%	35 865	2.73
1976	1 965	5 052	50.9%	795	8.0%	3 832	38.6%	181	1.8%	62	0.6%	9 922	5.05
1977	1 341	1 833	65.7%	619	22.2%	191	6.9%	91	3.3%	54	1.9%	2 788	2.08
1978	4 149	1 593	33.3%	1 110	23.2%	1 233	25.8%	812	17.0%	30	0.6%	4 778	1.15
1979	11 218	17 641	43.7%	2 188	5.4%	17 029	42.2%	3 342	8.3%	134	0.3%	40 334	3.60
1980	17 505	2 811	22.5%	1 519	12.1%	7 788	62.2%	393	3.1%	9	0.1%	12 520	0.72
Averages	5 972		24.0%		10.6%		54.7%		10.0%		0.9%	12 979	2.51

by FRI and ADFG and summarized in ADFG reports (see Bue 1985, which is latest in the series, for citations of earlier reports); (4) Air temperature data at King Salmon and Dillingham collected and summarized by U.S. Weather Service.

EVIDENCE FOR NON-FISHERY RELATED DEPENSATION

There are two direct methods to evaluate depensation. One is based on estimates of return from parent escapement and the other based on estimates of smolts produced from parent

TABLE 2. Escapement, return, return/spawner, smolts produced, and smolts per spawner for Kvichak River sockeye by peak-, pre-, post-, and other-cycle years.

	Brood year	Escapement (millions)	Return (Including high seas catches) (millions)	Return per spawner	Number of smolts produced (millions)	Smolts per spawner
Peak-Cycle	1952	6	21	3.5	—	—
	56	9.4	38.8	4.1	—	—
	60	14.6	54.4	3.7	—	—
	65	24.3	43.5	1.8	—	—
	70	13.9	15.7	1.1	195.2	14.0
	75	13.1	35.9	2.7	291.7	22.3
	80	17.5	12.5	0.7	226.7	13.0
			Mean	2.5		16.4
			Median	2.7		14.0
Pre-Peak	1955	0.3	1.5	5.0	—	—
	59	0.7	0.5	0.7	—	—
	64	1	5.5	5.5	—	—
	69	8.4	5.3	0.6	139.8	16.6
	74	4.4	25.6	5.8	222.6	50.6
	79	11.2	40.3	3.6	309.2	27.6
			Mean	3.5		31.6
			Median	4.3		27.6

TABLE 2. (*Continued.*)

	Brood year	Escapement (millions)	Return (Including high seas catches) (millions)	Return per spawner	Number of smolts produced (millions)	Smolts per spawner
Post-Peak	53	0.3	0.6	2.0	—	—
	57	3	4	1.3	—	—
	61	3.7	3.4	0.9	—	—
	66	3.8	6.1	1.6	—	—
	71	2.4	2.8	1.2	26.5	11.0
	76	2	9.9	5.0	58.6	29.3
	81	1.8	—	—	44.1	24.5
			Mean	2.0		21.6
			Median	1.8		24.5
Other Years	54	0.2	0.8	4.0	—	—
	58	0.5	0.3	0.6	—	—
	62	2.6	5.2	2.0	—	—
	63	0.3	1	3.3	—	—
	67	3.2	1.4	0.4	—	—
	68	2.6	0.5	0.2	—	—
	72	1	1.9	1.9	8.5	8.5
	73	0.2	2.4	12.0	12.9	64.5
	77	1.3	2.8	2.2	39.2	30.2
	78	4.1	4.8	1.2	214.7	52.4
	82	1.1	—	—	53.8	48.9
			Mean	2.8		40.9
			Median	1.6		48.7

escapement. Returns per spawner for the 1952–80 brood years were evaluated by cycle year (Table 2). No significant differences in return per spawner among peak, post-peak, pre-peak, and other cycle brood years were found (Kruskal-Wallis one-way analysis of variance, P = 0.66), consequently no depensation or direct suppression of returns in certain cycle year escapements can be inferred from these data. Also there was little evidence for compensation (i.e., lower return per spawner for large escapements) in the Kvichak return per spawner data.

Hydroacoustic estimates of smolt abundance (Menin and Paulus 1975) were available for 1969–82 brood years (Table 2). Peak cycle brood years produced significantly fewer smolts per spawner than did other brood years (Wilcoxon rank sum test, P<0.01). A greater degree of compensation was apparent in the smolt production than in adult production from parent escapement. No evidence of depensation exists in the Kvichak smolt production data. The smolt production for the 1969–72 brood years was much lower than in later brood years (Fig.4). Adult production from these brood years was depressed in other Bristol Bay systems (Eggers et al. 1984) and was presumably due to unfavorable environmental conditions (Rogers 1984). Smolts from the 1973–82 brood years followed closely the expected production of a simple compensative reproduction curve (Ricker 1954).

Kvichak smolts produced by large escapements were smaller than those produced from smaller escapements (Fig. 5). Age 1. smolts from post-peak cycle brood years were smaller than those observed for other brood years of comparable escapement (Fig. 5). Presumably, this was due to competition with age 2. progeny from the peak cycle brood

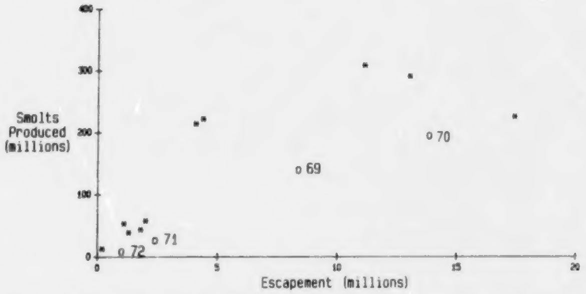

FIG. 4. Estimated numbers of outmigrating sockeye salmon smolts plotted against parent escapement, 1969–82 brood years, for the Kvichak River (Asterisks denote brood years 1973–82).

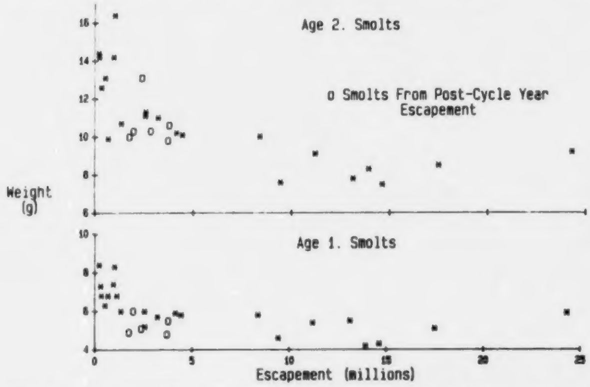

FIG. 5. Mean weights of age 2. (A) and age 1. (B) Kvichak River sockeye salmon smolts plotted agains 1953–82 parent escapements. Open circles represent weights from post-cycle brood years (57, 62, 66, 71, 76, and 81).

year escapement. This pattern did not hold as well for age 2. smolts from post-peak cycle brood years. There appears to be very little difference in the size of smolts produced from escapements over 5 million (Fig. 5). This may reflect the mitigation of density effects by fertilization of the lake by salmon carcasses, and/or that escapements over 5 million have tended to produce smolt populations of comparable magnitudes (Fig. 4).

Density dependent growth effects were not readily apparent in the Kvichak adult production from parent escapements. Koenings and Burkett (1987) found that size of sockeye smolts was inversely related to the density of juveniles in nursery lakes. However, in their study, mortality did not increase until smolt weight fell below a 2 g threshold and Kvichak smolts were well above the 2 g threshold. If the threshold identified by Koenings and Burkett applied for the Kvichak, then the observed density dependent size of smolts was consistent with the weak compensation observed in the returns from parent escapement.

Kvichak production has been depressed for brood years immediately following large escapements. Both return per spawner for 1956–80 brood years in which escapements were over 2.4 million and smolts per spawner for 1969–82 brood years were inversely related to the magnitude of escapement the previous brood year (Fig. 6). There were no differences **in this relationship among pre-peak, post-peak, and other cycle years (Fig. 6). This indicated that cycle year interactions (Ward and Larkin 1964) occured in the Kvichak and may have contributed to the cyclic nature of the Kvichak runs.**

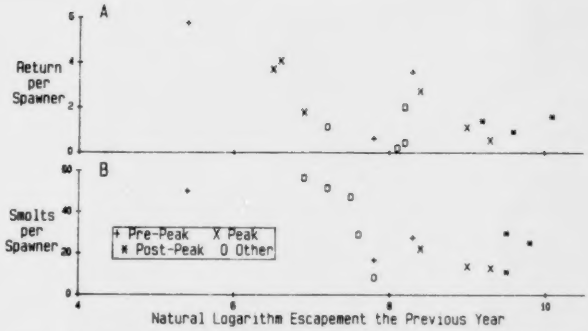

FIG. 6. Return per spawner (A) and smolts per spawner (B) for Kvichak River sockeye plotted against the natural logarithm of escapement the previous brood year. + are pre-peak. X are peak. * are post-peak, and 0 are other cycle brood years.

EVIDENCE FOR DEPENSATORY FISHING

Rates of exploitation on the Kvichak return were compared by peak, pre-peak, post-peak, and other cycle run years (Table 3). Significant differences in exploitation rate existed among cycle years (Kruskal–Wallis analysis of variance, $P < 0.05$). The rate of exploitation for the pre-peak and peak cycle years tended to be lower than average, whereas that for the post-peak cycle years tended to be much greater than average. Within other cycle years, large returns (those greater than 3 million) tended to be exploited at a much higher rate (mean = 53.3%) than small returns (mean = 17.4%).

TABLE 3. Inshore run, escapement, inshore catch, target rate of exploitation (U), realized rate of exploitation, and management error for Kvichak River, by peak-cycle, pre-cycle, post-cycle, and other-cycle return years.

	Return year	Inshore run (millions)	Escapement (millions)	Inshore catch (millions)	Escapement goal (millions)	(1) Target U (%)	(2) Realized U (%)	(2)-(1) Error (%)
Peak-Cycle	1956	15.000	9.440	5.560	—	—	37%	—
	60	24.880	14.630	10.250	—	—	41%	—
	65	42.112	24.326	17.786	8.000	81%	42%	−39%
	70	30.517	13.935	16.582	19.000	38%	54%	17%
	75	14.747	13.140	1.606	14.000	5%	11%	6%
	80	35.234	22.505[a]	12.729	14.000	60%	36%	−24%
	85	13.451	7.211	6.240	10.000	26%	46%	21%
						Means	38%	−3%
						Median	41%	
Pre-Peak	59	1.000	0.680	0.320	—	—	32%	—
	64	1.721	0.957	0.764	5.000	0%	44%	44%
	69	12.155	8.394	3.761	6.000	51%	31%	−20%
	74	4.582	4.443	0.139	6.000	0%	3%	3%
	79	24.637	11.218	13.419	6.000	76%	54%	−21%
	84	22.870	10.491	12.379	10.000	56%	54%	−2%
						Means	36%	1%
						Median	38%	
Post-Peak	57	10.620	2.840	7.780	—	—	73%	—
	61	14.110	3.710	10.400	—	—	74%	—
	66	7.944	3.775	4.169	6.000	24%	52%	28%
	71	6.152	2.387	3.765	2.500	59%	61%	2%
	76	3.423	1.965	1.458	2.000	42%	43%	1%
	81	6.960	1.754	5.206	2.000	71%	75%	4%
						Means	63%	9%
						Median	67%	

TABLE 3. (*Continued.*)

	Return year	Inshore run (millions)	Escapement (millions)	Inshore catch (millions)	Escapement goal (millions)	(1) Target U (%)	(2) Realized U (%)	(2)-(1) Error (%)
Other Years	58	1.160	0.530	0.630	—	—	54%	—
	62	4.414	2.581	1.833	2.500	43%	42%	−2%
	63	0.562	0.339	0.223	0.750	0%	40%	40%
	67	5.017	3.216	1.801	3.500	30%	36%	6%
	68	2.945	2.557	0.388	0.874	70%	13%	−57%
	72	1.352	1.010	0.342	2.000	0%	25%	25%
	73	0.248	0.227	0.021	2.000	0%	8%	8%
	77	2.081	1.341	0.740	2.000	4%	36%	32%
	78	7.965	4.149	3.816	2.000	75%	48%	−27%
	82	3.022	1.135	1.887	2.000	34%	62%	29%
	83	19.922	3.570	16.352	2.000	90%	82%	−8%
						Means	41%	5%
						Median	40%	
Means (all years)		11.36	5.95	5.41	5.42	0.39	0.44	0.03
SD (all years)		11.18	6.41	6.64			19.7%	25.1

[a] Effective escapement for the 1980 brood year was 17.505 million. Approximately 5 million sockeye were unable to spawn because of high discharge velocity barrier to upstream migration in the Newhalen River.

Under the management strategy employed from 1956 to the present, the Naknek/Kvichak fishery has exerted highly depensatory mortality on Kvichak runs. The high seas fishery may have reinforced the depensatory manner in which Kvichak sockeye were exploited. The fishery targeted heavily on sockeye during years when the progeny of Kvichak peak cycle brood years were at sea (Rogers 1987; Fredin et al. 1977). Because of the great abundance of the age .2 component of the peak cycle year returns and finite capacity of the high seas fishery, the high seas fishing mortality, even with the targeting, was most likely lower on peak cycle year runs. However, the age .3 component of the peak cycle year runs was exploited in high seas fisheries both as age .1 and age .2 immatures. Because the age .3 component of the peak cycle returns is much smaller than the age .2 component (see following age at maturity submodel), the limited capacity of the high seas fleet was presumably less of a factor. With the targeting of the high seas fishery on the peak cycle progeny, both the age .3 component of peak cycle returns and the age .2 component of post-peak returns may have received greater high seas exploitation rates.

The early fishery (before adoption of formal escapement goals) was very likely depensatory in nature. As mentioned above, it was limited by processing capacity and only loosely regulated for a fifty percent exploitation rate. We hypothesize that effects of these early, quotalike, fisheries were very analogous to those of the lacustrine predators postulated by Ricker (1950) and others as the depensatory agent maintaining cyclic dominance in the Fraser River sockeye. The early fishery also utilized larger mesh gill nets, which tended to select age .3 sockeye (Mathisen 1979; Rogers 1987). This resulted in the highest exploitation of the post-peak cycle year runs, which were mostly the age .3 component of the peak cycle return.

Native subsistence fisheries existed in Bristol Bay prior to today's fishery. Native fisheries have been shown to be depensatory in nature and may have contributed to cyclic dominance observed in the Fraser sockeye (Peterman 1980). However, native fisheries in Bristol Bay may not have been at levels that could have significantly affected escapement levels.

DISCUSSION OF DEPENSATORY PROCESSES

In summary, little direct evidence was found for fishery independent depensation in the population biology of Kvichak sockeye. However, there was significant indirect evidence for depensation, in that high escapements in the preceding brood year tended to depress production in the current brood year and the growth of age 1. smolts was suppressed in post-cycle brood years. However, these effects have not been manifested in a statistically significant lower return per spawner for post-cycle brood years. There was weak evidence for compensation in the return per spawner data and stronger evidence for compensation in the smolts per spawner data.

The historical fishing pattern on the Kvichak sockeye was extremely depensatory. The review of information above suggested that depensatory fishing in conjunction with the suppression of production following large escapements has created and maintained the Kvichak cycle. We know of no studies that have critically evaluated the hypothesis that depensatory fishing can create and maintain cycles in returns of sockeye salmon populations. The task in the model identification sections of this study is to use historical patterns of returns to the Kvichak to test the brood year interaction/depensatory fishing hypothesis.

Model Identification

Our computer simulation study is similar to earlier studies of Adams River sockeye (Ward and Larkin 1964; Larkin 1971) and of Skeena River sockeye (Larkin and McDonald 1968), but differs in that the model is more empirical in nature. We have avoided the use of theoretically complex models incorporating multi-stage growth curves with varying degrees of depensation, compensation, and stochastic multipliers (e.g., Paulik 1973; Peterman 1977). These models have many implicit assumptions that cannot be verified and a multitude of parameters that cannot be estimated easily. It is relatively easy to tune the more complex models to fit the historical data, and this ability is, at best, weak verification of the implicit hypotheses.

Our approach more closely follows the recommendations of Larkin (1973). The model is simple, minimizing implicit assumptions and reflects only the past associations in the data. The stochastic realities of the data, including autocorrelation with respect to time have been addressed and all parameters were estimated at the model identification stage.

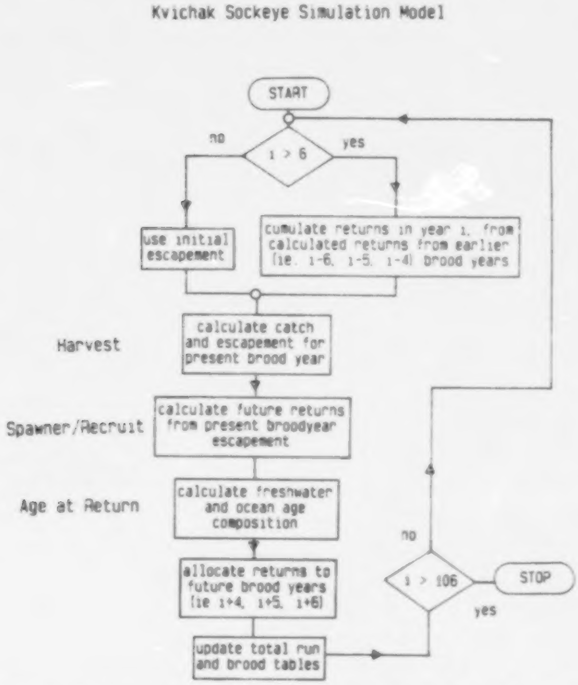
Kvichak Sockeye Simulation Model
START
no
ı > 6
yes
use ınitıal escapement
cumulate returns ın year ı, from calculated returns from earlier (ie. ı-6, ı-5, ı-4) brood years
Harvest
calculate catch and escapement for present brood year
Spawner/Recruit
calculate future returns from present broodyear escapement
Age at Return
calculate freshwater and ocean age composition
allocate returns to future brood years (ie ı+4, ı+5, ı+6)
update total run and brood tables
no
ı > 106
yes
STOP

FIG. 7. Elements of the model used to simulate the effects of fishing on returns of sockeye salmon to the Kvichak River.

The model plan (Fig. 7) was a single stock version of that proposed by Larkin and Hourston (1964). The form of the model is a computer program that recursively constructs the current run from production of previous brood years, allocates the run to catch and escapement, then projects the future year returns from that escapement. For each year simulated, the returns constituting the run are collected. The Kvichak run consists of four major age classes from three brood years, including 1.2 (age 4), 2.2 (age 5), 1.3 (age 5), and 2.3 (age 6) (the European method (Koo 1962) of age designation is used throughout this paper). The run is then allocated to catch and escapement based on a harvest submodel. The total returns from a given escapement are calculated using the spawner/recruit submodel. The total returns are then allocated to specific age classes and future run years based on age at return submodel. In the initial stages of the simulation there is no history of production and escapements are arbitrarily taken to be 10 million. Beginning with the 7 th year, the run construction is based on simulated production from previous brood years. It is necessary to keep track of peak-cycle years in the model because cyclic harvest policies are conditioned on the current year relative to the peak cycle year. Because of variable age at maturity, the cyclic harvest policy must be phased with the cycle of resulting runs. This was accomplished by having the interval of time between a current peak cycle year and the next depend on the freshwater age of the return from the current peak cycle year. The interval will be either four or five years if the freshwater age is 1. or 2., respectively. Note that this phasing scheme is feasible since the freshwater age of the peak cycle return can be estimated two years prior to the peak cycle run based on estimates of numbers of smolts produced from peak-cycle brood years.

Random numbers were used throughout the model to mimic natural variation. These were generated using the multiplicative congruential method (Carnahan et al. 1969) with the largest modulus possible within the integer size limitation (32 bit integers) of the hardware used. The random number generator gave good adherence to the uniform distribution and no significant autocorrelation was found in the sequences of generated numbers. Note that the uniform random variables were converted on the basis of empirically derived probability distributions to reflect the respective natural variation. The biology implicit in the model will be apparent after presentation of the spawner/recruit, age at return, and harvest submodels.

SPAWNER/RECRUIT SUBMODEL

The Kvichak escapement–return data are critical for developing the spawner/recruit submodel. Kvichak sockeye are harvested jointly with those bound for the Naknek and Branch Rivers. Naknek–Kvichak district catches were allocated to these systems based on the relative escapement magnitudes by age class. This method will give accurate catch allocations provided that for each age class no differences in run timing or catchability exist among consitutent stocks. (Dr. David Bernard personal communication, Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK 99518). In general, these assumptions were met for river systems terminating in the Naknek–Kvichak district. Recent studies where Naknek–Kvichak district catches were allocated using scale pattern analysis (cf. Marshall et al. 1987) gave results consistent with catch allocations based on relative escapement magnitudes by age (Dr. Steven Fried personal communication, Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK 99518).

Of more concern was the potential interception of sockeye bound for the Kvichak in the Egegik and Ugashik fishing districts (Fig. 1), since Kvichak fish caught in these districts would be allocated to the respective river systems and would not be included in the Kvichak production. Early tagging studies (Pennoyer and Nelson 1967; Straty 1969) showed that very few sockeye bound for river systems of the Nushagak district were caught in the eastside districts (Naknek–Kvichak, Egegik, and Ugashik), and vice versa. The early tagging studies also showed that a much greater intermingling of stocks occurred among the eastside fishing districts. Fish caught in the several districts were primarily destined to the respective terminal river systems; however, fish bound for all other eastside river systems were intercepted in all of the eastside fishing districts.

There was a high correlation ($\rho = 0.72$) in return per spawner between the pooled westside river systems (i.e., the constituent stocks exploited in the Nushagak district) and the pooled eastside river systems (Fig. 8). This observation suggested that production was synchronized among river systems, presumably due to environmental factors operating on a scale larger than the Bristol Bay Area. There was a much poorer correlation in return per spawner between the Naknek–Kvichak and the Egegik–Ugashik River systems ($\rho = 0.40$) (Fig.9). This reduced synchrony in production among river systems of the Naknek–Kvichak and Egegik-Ugashik districts was presumably due, in part, to incorrect catch allocation. The return per spawner in the Egegik-Ugashik River systems has been much higher than in the Naknek–Kvichak River systems for recent brood years (1976–80) (Fig. 9). There has been an increase in fishing effort, beginning in 1980, in the Egegik and Ugashik districts (Fig. 10), in response to recent large returns to both the Egegik and Ugashik River systems. Increased interception of Kvichak fish resulting from these changes in fishing patterns may have contributed to the recent divergence in apparent production between the Egegik–Ugashik and the Naknek–Kvichak River systems (Fig. 9).

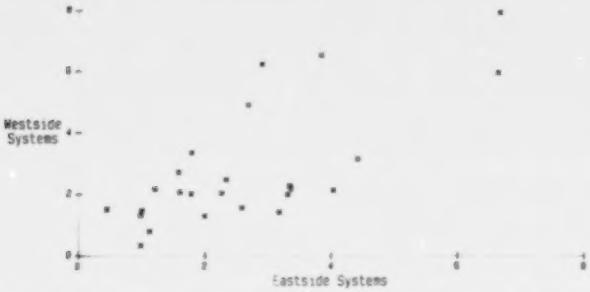

FIG. 8. Return per spawner observed for pooled westside river systems (Wood, Nuyakuk, Igushik, and Nushagak-Mulchatna) plotted against return per spawner observed for the pooled eastside river systems (Kvichak, Branch, Naknek, Egegik, and Ugashik Rivers), 1956–80 brood years.

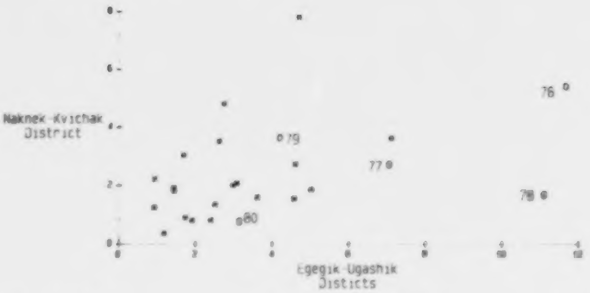

FIG. 9. Return per spawner observed for pooled river systems terminating in Naknek/Kvichak fishing district (Kvichak, Branch, and Naknek Rivers) plotted against return per spawner observed for pooled river systems terminating in Egegik/Ugashik fishing districts (Egegik and Ugashik Rivers), 1956–80 brood years. Data for 1956–75 brood years indicated by asterisks.

Because the eastside and westside runs were spatially separated, the catches in the eastside districts were correctly allocated to the eastside river systems. Data for all of the eastside river systems were pooled, and the observed deviation from the pooled eastside return per spawner for the Naknek/Kvichak River systems was compared to that observed for the Egegik/Ugashik River systems (Fig. 11) by brood year. The deviation in return per spawner (R/S) for the Naknek/Kvichak River systems is low for pre-peak, peak, post-peak, and the early 1970 brood years. These were brood

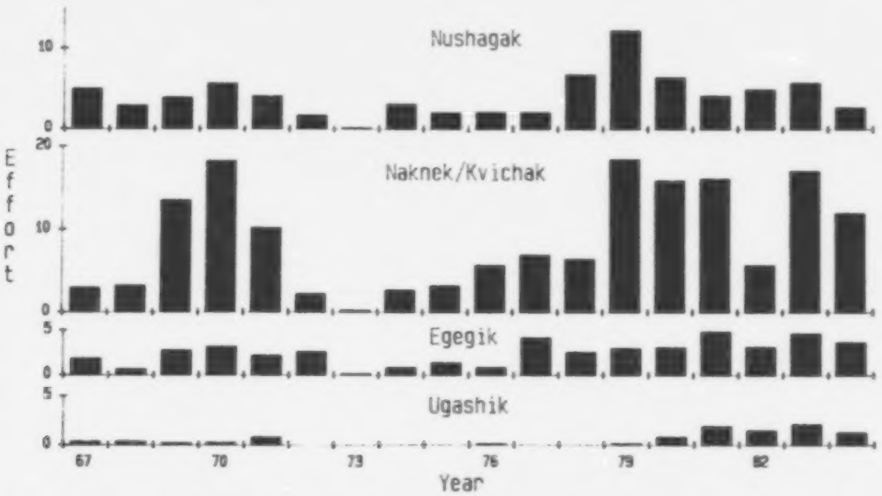

FIG. 10. Fishing effort (thousands of boat days) for Nushagak, Naknek/Kvichak, Egegik, and Ugashik fishing districts, 1967–84. Data from Bristol Bay Area Annual Management Reports (Unpublished reports with restricted distribution, Alaska Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Rd., Anchorage, AK 99518), values 1967–75 based on post-season computer summaries of fish tickets, values 1976–84, based on in-season aerial surveys of fishing effort.

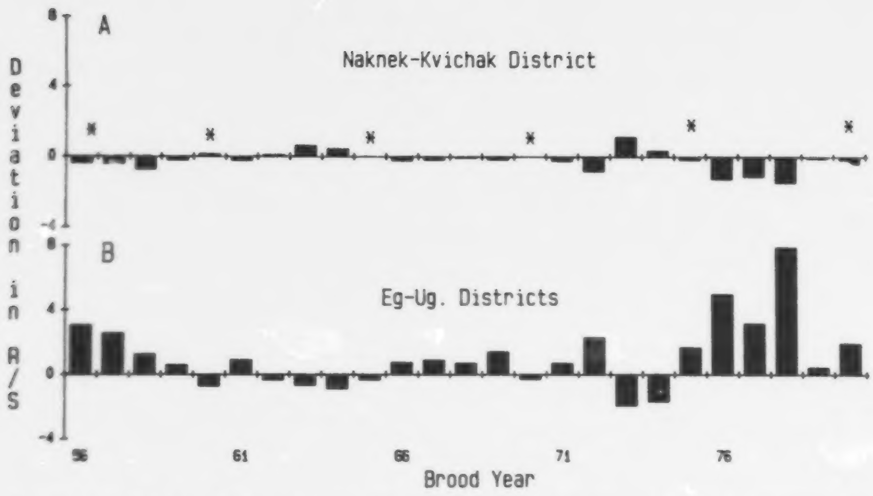

FIG. 11. (A) Deviation by brood year from pooled eastside river systems return per spawner, for pooled river systems terminating in the Naknek/Kvichak district, and (B) for pooled river systems terminating in the Egegik/Ugashik districts. Kvichak cycle brood years are indicated by asterisks.

years of large Kvichak return or brood years which had very restricted fishing. In years of large Kvichak runs, there was lower fishing effort in the Egegik/Ugashik districts relative to the Naknek/Kvichak district (Fig. 10) since fishing was concentrated in the Naknek/Kvichak district to harvest the large Kvichak run. In these years errors in catch allocation are small relative to the size of the Kvichak return.

However, during years of low Kvichak run fishing effort was more dispersed among Bristol Bay fishing districts (Fig. 10). In off-cycle brood years, except for those in the early 1970's when fishing was reduced substantially in Bristol Bay, there was greater deviation in R/S from the pooled eastside R/S, in both the Naknek/Kvichak River systems and Egegik/Ugashik River systems (Fig. 11). This greater deviation in R/S during off peak-cycle return years was presumably due to greater interception by the increased fishing effort in the Egegik/Ugashik districts.

Because of the relatively large Kvichak return and directed fishery, errors in catch allocation have not appreciably affected the integrity of the Kvichak escapement–return data for most brood years. The interception rate of Kvichak fish in the Egegik and Ugashik districts appeared to be greater in years of low Kvichak return. Thus, the apparent return per spawner from the escapement–return data for these brood years would be, on the average, lower than what had actually occurred, due to incorrect catch allocation.

We used three criteria in developing a reproduction curve for the spawner recruit submodel: first, it must pass through the origin; second, the return must approach zero as the escapement approaches infinity; and third, the escapement during the previous year must be incorporated to reflect the depression of production following large escapements observed in the Kvichak data. The first and second criteria were necessary to bound the model predictions, and were consistent with observations that natural populations can go extinct and do not increase without limit (Thompson 1962).

The following model is consistent with the above criteria and was used to calculate return (R_t) from parent escapement (S_t) and escapement of the previous brood year (S_{t-1}).

$$[1] \qquad R_t = S_t \, \alpha e^{-\beta S} \gamma_1 S_{t-1} - \gamma_2$$

Where α, β, γ_1, γ_2 are parameters estimated by a two stage procedure. For a given level of escapement the previous brood year equation 1 reduces to a simple compensative reproduction curve (Fig. 12), and meets criteria 1 and 2 above. Equation 1 is consistent with the evidence for compensation observed in the numbers of smolt produced from various escapement levels in the Kvichak, 1969–82 brood years. In the model, production is depressed in brood years following years of large escapement.

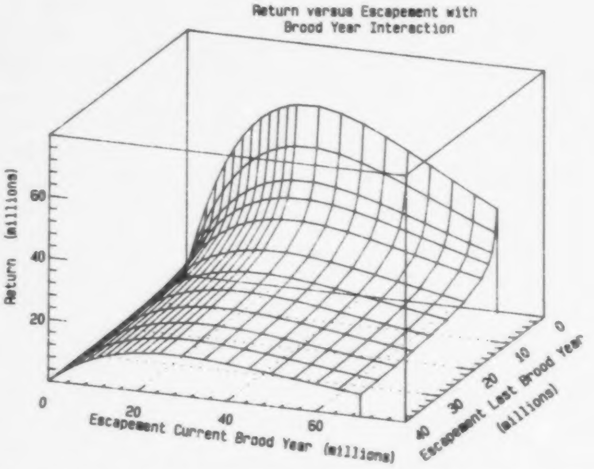

FIG. 12. Plot of the spawner recruit submodel (eq. 1 in text) estimated for Kvichak River sockeye. Return is plotted against current brood years escapement and previous brood year escapement.

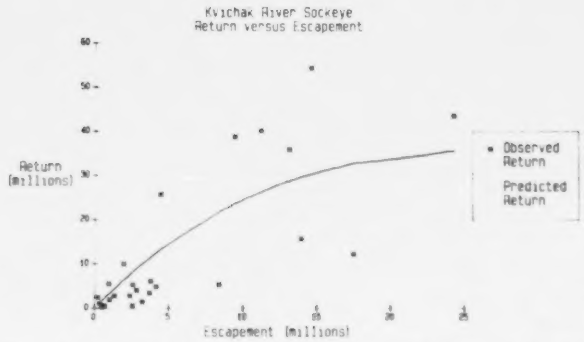

FIG. 13. Returns plotted against parent escapement, 1956–80 brood years, together with fitted simple compensative reproduction curve (eq. 2 in text).

In the first stage of the procedure used to estimate parameters in equation 1, a simple compensative reproduction curve (Ricker 1954) was fitted to the Kvichak return from escapement data for the 1956–80 brood years (Fig. 13), using a simple search over the parameter space to minimize residual squared deviations in untransformed units ($R^2 = .604$).

$$[2] \quad R_i = S_i\,\alpha\,e^{-\beta S}$$

In equation 2, R_i = return, S_i = escapement, α, β are parameters with values 3.5, and −0.000035, respectively. The residuals of the simple compensative model were inversely related to the escapement the previous brood year (Fig. 14). This reflected the depressed production of brood years following large escapements. Note that for brood years where the allocated returns to other eastside river systems were more than twice the allocated returns to the Kvichak, the residual ln (R/S) was much lower. We felt that this anomalous low production reflected errors in catch allocation and, therefore, inclusion of those data would give a biased spawner recruit model. These were excluded when using the full model (eq. 1) with the brood year interaction terms included. In the second stage, γ_1, γ_2 were estimated by regressing the residuals of the simple compensative model against the natural logarithm of escapement the previous brood year, that is:

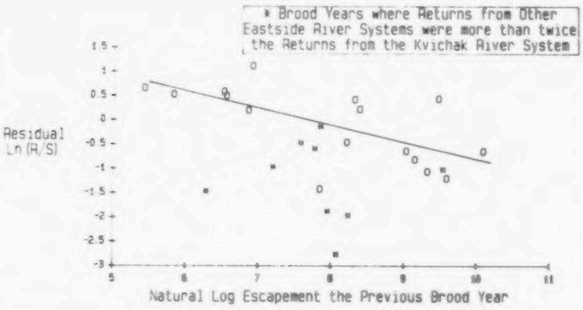

FIG. 14. Residuals (predicted ln(R/S) — observed ln(R/S) for the simple compensative reproduction curve (open circles) plotted against natural logarithm escapement the previous brood year, together with the fitted regression line (eq. 3 in text). Asterisks indicate brood years of low Kvichak return relative to other eastside systems and were excluded in estimating eq. 3.

$$[3] \quad \ln\left\{\frac{R_i}{S_i}\right\} - [\ln\alpha - \beta S_i] = \ln\gamma_1 + \gamma_2 S_{i-1} + e_i$$

The estimated values for γ_1, γ_2 were 15.1 and −0.353, respectively, and the R^2 for the full model in untransformed units was 0.81. In escapement-return data for other sockeye systems, return per spawner ratios tended to have a log-normal probability distribution (Allen 1973). We used log normal random deviates (e_i) to simulate departures from R/S predicted by equation 1. Because years of low Kvichak return relative to other eastside systems were excluded to correct bias, the mean of the residuals was not zero, and the variance was not constant with respect to escapement (Fig. 15). We corrected this problem by assuming that the residual ln (R/S) has a normal probability distribution for which the mean and variance depended on level of escapement. Based on the empirical relationship between observed residuals and escapements (Fig. 15), the mean (m) increased linearly ($m = -0.677 + (4.03 \times 10^{-5})\,S_i$) to zero for escapements less than 15 million, and for larger escapements the mean was equal to zero. Again based on the observed residuals the standard deviation of residual ln (R/S) (e_i) decreased with escapement (Std. Dev.$(e_i)) = 1.07 \exp((-3.53 \times 10^{-5})\,S_i)$).

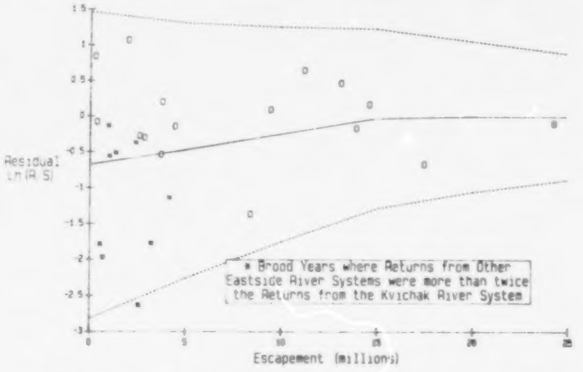

FIG. 15. Residuals [predicted ln(R/S — observed ln (R/S)] for the full spawner recruit submodel (Fig. 12), plotted against parent escapement. Also shown are the mean (solid line) and upper and lower confidence bounds (±2 SD) (dashed lines).

With the error structure defined above, the model will reflect accurately the historical patterns of production, provided escapement magnitudes are within the limits of historical observation. The tendency for the residual ln(R/S) to be negative for low escapements (Fig. 15) reflects the method used to correct for bias in Kvichak escapement–return data due to errors in catch allocation. The effect of this would be depensatory as implied in the spawner recruit submodel. In using the model to evaluate alternative harvest policies, the effect could be considered as depensatory fishing not implicit in the particular harvest policy evaluated, due to interception in other eastside fishing districts.

AGE AT RETURN SUBMODEL

Numbers and age composition of the Kvichak sockeye return have been available for all runs beginning in 1956. Prior to this, age composition data were available only for the Naknek–Kvichak district catches. During the recent period (after 1956) age .2 fish have been dominant in the Kvichak return. Returns from large escapements tended to have a lower proportion of age .3 fish than returns from small escapements. Freshwater age has been more variable than ocean age but returns from cycle year escapements have tended to occur in a single year. Because the freshwater age has shifted from 1. to 2., the period of the cycle has changed from 4 year to 5 years, respectively. Age at maturity and factors that drive this variable are fundamental to understanding the Kvichak cycle, and quantitative aspects of this problem are addressed below.

In the Kvichak, freshwater age appears to be determined by environmental conditions in the lacustrine phase of the sockeye life history (Rogers 1984, 1986; Rogers and Poe 1984). Brood years which experienced unusually warm weather during lacustrine residence produced a higher proportion of age 1 smolts. For instance, the 1952 and 1956 brood years experienced high temperatures and produced largely 1.2 returns, whereas the 1960, 1965, 1970, and 1975 brood years experienced cold temperatures and produced largely 2.2 returns (Fig. 16). Note that temperature was indexed by the anomaly (deviation from long-term monthly average) in Bristol Bay (Sum of Dillingham and King Salmon) monthly air temperatures. For each brood year (i), the anomalies were summed for the months of lacustrine growth of age 1. smolts, that is, April–October in year $i+1$ and April–May in year $i+2$. There was a high correlation between freshwater age (expressed as proportion of 1. age fish) in the Kvichak return in 1952–1980 brood years (Fig. 17) and air temperature ($\rho = 0.716$). There was also a significant but lower correlation between freshwater age in the Naknek/Kvichak catches from the 1918–51 brood years and air temperature ($\rho = 0.380$), as well as the freshwater age of smolts produced from the 1969–1982 brood years and air temperature ($\rho = 0.695$).

There was a slight inverse correlation between freshwater age and numbers in the escapement ($\rho = -0.171$). A simple multiple regression model was fitted ($R^2 = 0.524$) to the freshwater age composition of the Kvichak return from the 1952–80 brood years (Fig. 17).

$$Y = 41.35 + 18.5\,T - 0.412\,S + e_i \qquad (4)$$

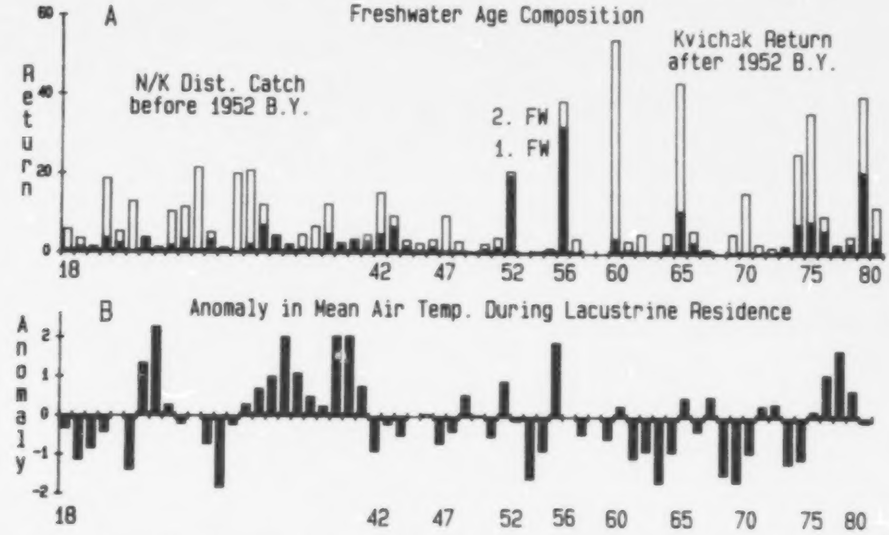

FIG. 16. (A) Naknek-Kvichak district catches, 1918–51 brood years, and Kvichak total return, 1952–80 brood years all by 1. and 2. freshwater age. Return years are shown on the abscissa. (B) Bristol Bay air temperature index (see text for definition) during lacustrine phase, 1918–80 brood years. Cycle years from 1942 to 1980 are noted on the abscissa.

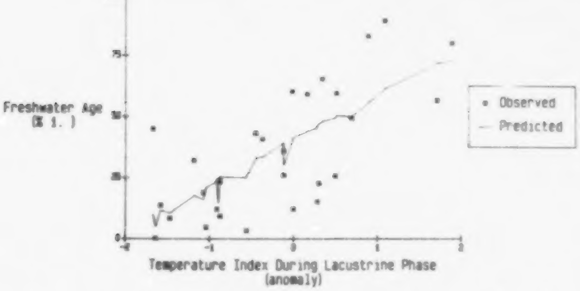

FIG. 17. Relationship between freshwater age (% 1.) of Kvichak returns and temperature index shown in Fig. 16B. Plotted are equation 4, showing second-order effect of escapement, and observed values, 1952–80 brood years.

where Y = proportion age 1., T = temperature index, S = escapement, and e_i is the random deviation about the regression line. The mean of the residuals was zero and the variance was constant with respect to each of the independent variables. Thus, random normal deviates (mean = 0, standard deviation = 18.2%) were used to simulate the natural variability.

The time series of air temperature indices had a significant autocorrelation for a lag of 1 yr and no significant autocorrelations for higher lags. Here, temperatures of a given brood year somewhat influenced those experienced by the succeeding brood year. This effect can be simulated with a first order moving average process time series model (Box and Jenkins 1976; Pankratz 1983). This model was fitted to the temperature time series and used to simulate temperatures during the lacustrine phase.

(5) $T_i = - P_1 a_{i-1} + a_i$

where $P_1 = 0.484$ and the a_{i-1}, a_i are random deviations in year $i - 1$ and i, respectively. The a_i's were normally distributed with mean = 0 and standard deviation = 0.902.

Rogers (1987) has suggested that in Bristol Bay sockeye salmon, ocean age is largely genetic, determined by the ocean age of the parents. Rogers (1987) also suggested that ocean age does have some environmental components, since within genetic lines age 2. smolts have a greater tendency to mature as age .2 adults than age 1. smolts. Presumably the larger age 2. smolts would grow faster in the ocean and tend to mature earlier than age 1. smolts. For the Kvichak returns, the proportion of age .3 fish decreased with increased escapements ($\rho = -0.499$) (Fig. 18). This reflected the tendency for peak-cycle brood years to produce lower proportions of age .3 returns. Also in the returns, the proportion of age .3 fish was related to the freshwater age of the returns ($\rho = .508$), and indicated a greater tendency of larger age 2. smolts to mature as age .2 fish (Rogers 1987). The following multiple regression model (Fig. 18) was fitted to the data ($R^2 = .579$):

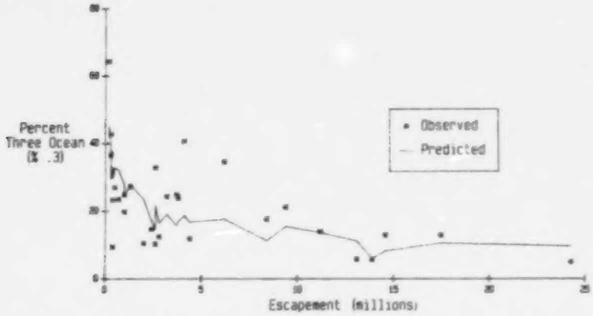

FIG. 18. Relationship between ocean age (% 3.) of Kvichak return and escapement. Plotted are equation 6, which incorporates second-order effect of freshwater age, and observed values, 1952–80 brood years.

(6) $\ln Y = 2.718 - 0.295 \ln S + 0.156 \ln F + e_i$

where Y = proportion age .3 fish in the return, S = escapement, F = proportion age 1., and e_i is the random deviation about the regression line. The mean of the residuals was zero and the variance was constant with respect to each of the independent variables. Thus, normal random deviates (mean = 0, standard deviation = 0.425) were used to simulate the natural variability.

In the Kvichak simulation model, simulated temperatures were first based on the time series model in equation 5, then temperatures were used with escapement to compute freshwater age based on equation 4, and finally freshwater age together with escapement were used to compute ocean age based on equation 6.

The empirical models of age at maturity developed here are consistent with Rogers' (1987) hypothesis regulating age at maturity in sockeye salmon. Kvichak cycle year escapements were large and tended to be from segregated brood lines. The effect of escapement, the dominant variable in the ocean age at maturity model, can be interpreted as genetic, reflecting the tendency of peak-cycle brood years to return as age .2 adults. The effect of freshwater age, the sub-dominant variable in the ocean age at maturity model, can be interpreted as environmental, reflecting the greater tendency of age 2. smolts to mature as age .2 fish.

Freshwater age was determined completely by environment in our model. The dominant variable in the freshwater age model is temperature. High temperature is indicative of lacustrine environmental conditions favorable to sockeye growth and earlier out-migration. The effect of escapement, the sub-dominant variable in the freshwater age model, can also be interpreted as environmental, reflecting the tendency of large escapements to produce a lower proportion of age 1. adults than would be expected based on temperature alone. Presumably this reflects the moderating effect of density dependent growth.

HARVEST SUBMODEL

Rarely have the pre-season escapement goals actually been achieved among the Bristol Bay river systems. This was due to a variety of factors, including low effort due to price disputes between fishermen and processors; inappropriate amounts of fishing time being allocated based on inaccurate assessments of run strength and/or run timing; and because of the constraints imposed by mixed stock fishing (Ricker 1958; Paulik et al. 1967). We have looked at the management error (*ER*), defined as the difference between the realized rate of exploitation (*U*) and the target rate of exploitation (*G*), for the Eastside River systems (Fig. 19). The latter quantity is the actual rate of exploitation necessary to achieve the pre-season escapement goal, that is:

$$G = (R - EG) / R$$

and $$ER = U - G$$

where R is the actual run and EG is the pre-season escapement goal. In general the frequency distributions of management error were very similar among the eastside river systems (Fig. 19). In years of poor run, when the run was greater than the goal, the management error was higher, (i.e., when ER is positive the realized rate of exploitation is higher than the target rate and the escapement achieved is lower than the goal). Poor runs have occurred more frequently for the Kvichak and Ugashik River systems. The returns to the Ugashik River were depressed from the the sixties to the mid-seventies, and many of the other cycle runs to the Kvichak were below escapement goals.

During years of poor run, the management error was consistently higher than in years of good run (one way analysis of variance, $P<0.01$). No significant differences existed among Eastside River systems in mean management error (one way analysis of variance, $P = 0.135$ all years; $P = 0.722$ when years of poor run were excluded).

Because no differences in management error were found among eastside river systems, the data were pooled and used to estimate probability distributions (Fig. 20). Because of the consistency in management error, it was possible to use a purely empirical model to simulate management error. Random deviates from the target rate of exploitation were computed based on these estimated probability distributions. Two cases were identified (Fig. 20) based on dif-

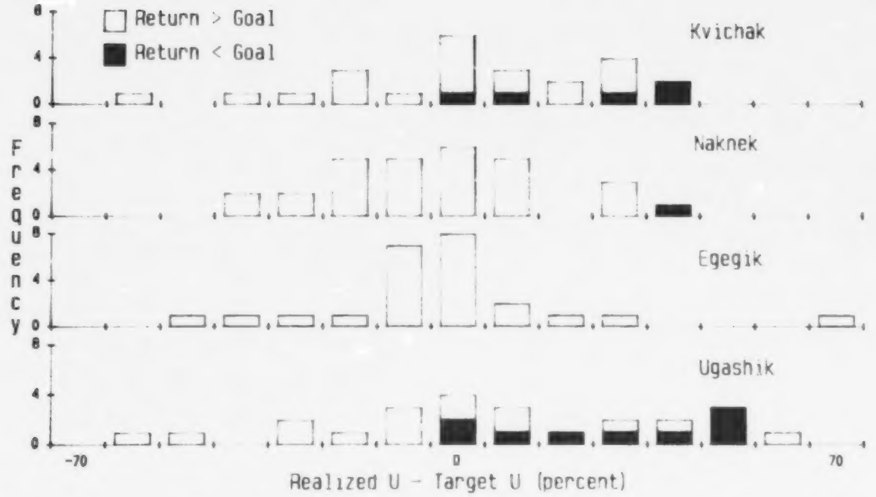

FIG. 19. Frequency distribution of management error (deviation from target rate of exploitation (G) in percent of total return, see text for complete definition) for each of the eastside river systems. Errors were stratified by years when the return was less than the escapement goal (solid) and years when the return was greater than the escapement goal (clear), 1962–85 return years.

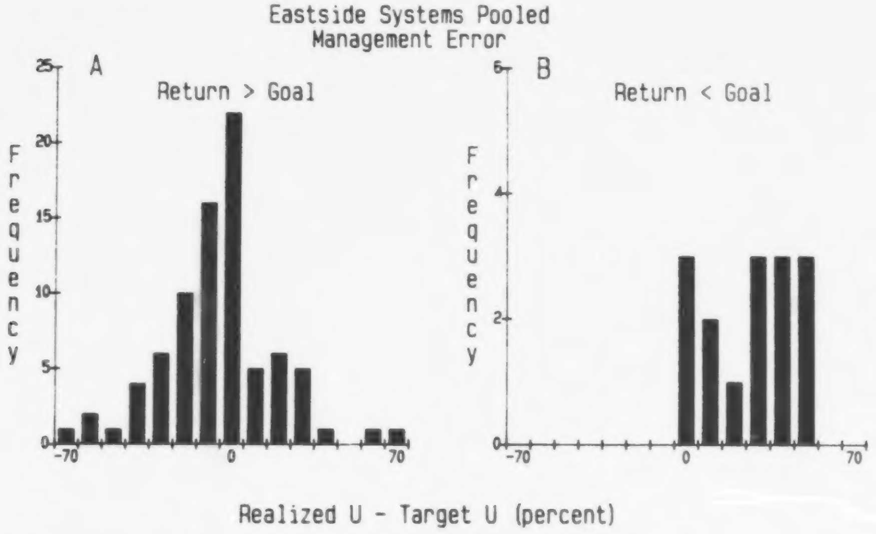

FIG. 20. Frequency distribution of management error (ER) for all eastside river systems pooled over 1962–85 return years. A, Years where return was greater than escapement goal, and B, years where return was less than escapement goal.

ferences identified in the analysis above. For years of good run, where the run was greater than the pre-season escapement goal (Fig. 20A), management error had a normal distribution (mean = −0.055, standard deviation = 0.0231). For years of poor run, management error had a uniform distribution on the interval zero to fifty percent (Fig. 20B). In the model, the target rate of exploitation based on implicit harvest policy was calculated, then modified according to the simulated management error based on the appropriate probability distributions in Fig. 20, as well as on run strength.

A salmon fishery managed for a fixed pre-season escapement goal is highly compensatory. Under this policy, the exploitation rate is high for large runs and low for poor runs. Differences in the nature of the management error observed for eastside river systems between years of poor and good run has tended to alter the compensatory nature of the fixed escapement goal management. This has contributed to the depensatory effects of the cyclic escapement goal policy under which the Kvichak was managed.

Model Evaluation

The Kvichak simulation model generated a 106-yr series of runs, catches, escapements, and returns by age for each brood year escapement (i.e., a complete brood table). The model was structured so that a variety of harvest policies could be evaluated. The initial escapements for the first 6 yr of the simulation were arbitrarily taken to be 10 million. The initial 20 yr were ignored in all simulations to prevent effects relating to the arbitrary initial conditions from biasing interpretation. In the subsequent analysis, 150 sample simulations were generated for each harvest policy. Note that for each simulation the average was taken over the last 86 yr.

We considered the Kvichak simulation model as a synthesis of individual submodels identified above. The model was evaluated by comparing simulated frequency distributions of several population parameters to those observed for the Kvichak sockeye (Fig. 21). The frequency distributions shown in Fig. 21 were generated with the status quo cyclic escapement goal harvest policy where goals for the peak cycle, pre-peak cycle, and other cycle years was 14 million, 6 million, and 2 million, respectively. Note that in the status quo harvest policy management was "imperfect" in that calculated departures from target escapements were based on randomly generated management error.

There was good agreement between simulated and observed frequency distributions for the ocean age (Fig. 21A) and freshwater age composition (Fig. 21B) of the return from brood year escapements, as well as the escapement (Fig. 21C), the total return (Fig. 21D), and the return per spawner (Fig. 21E). As expected in a stochastic model there was not perfect agreement between simulated and observed population parameters. The simulated distributions (Fig. 21)

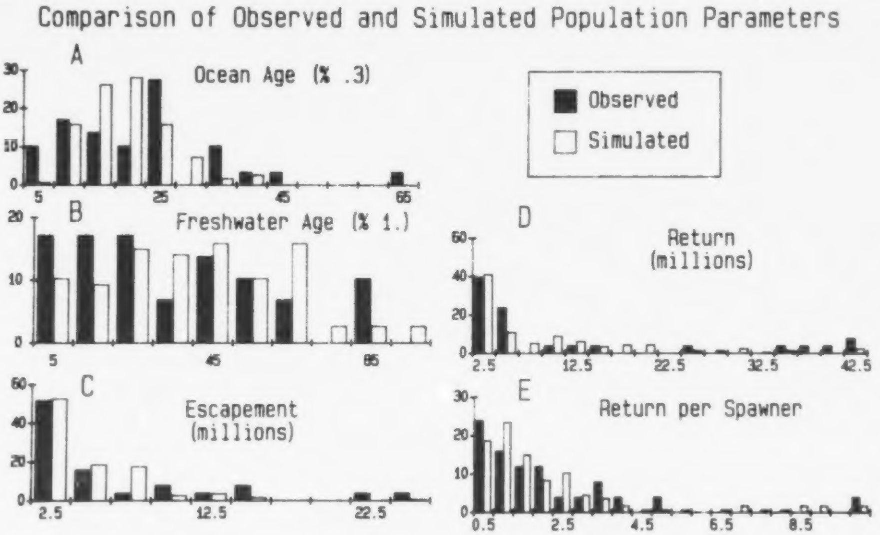

FIG. 21. Comparison of simulated frequency distributions (clear bars), using status quo harvest policy, and observed frequency distributions (solid bars) for the following population parameters: A. ocean age (% 3.), B. freshwater age (% 1.), C. escapement (millions), D. return (millions), and E. return per spawner for Kvichak River sockeye, 1952-80 brood years.

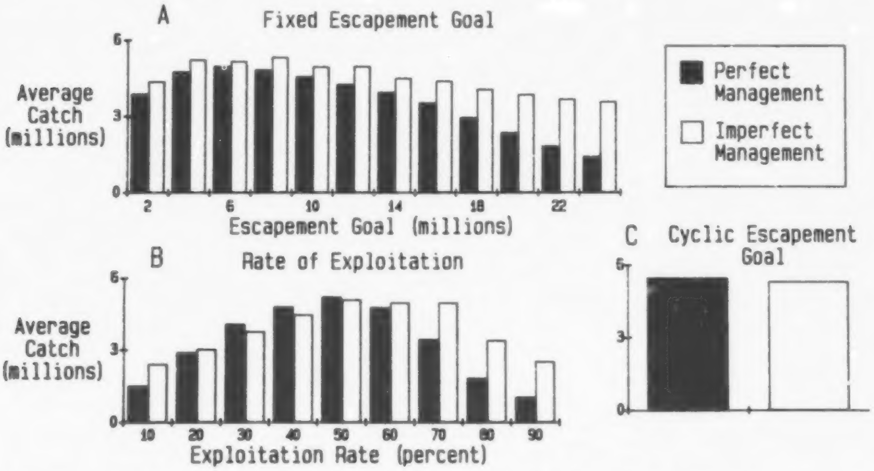

FIG. 22. Average catch (see text for definition of average) in simulated Kvichak runs managed under alternative harvest policies. A. Fixed escapement goal policy with goals from 2-24 million, and B. Rate of exploitation policy with rates from 10-90%. Both A and B are shown with perfect (solid bars) and imperfect (clear bars) management.

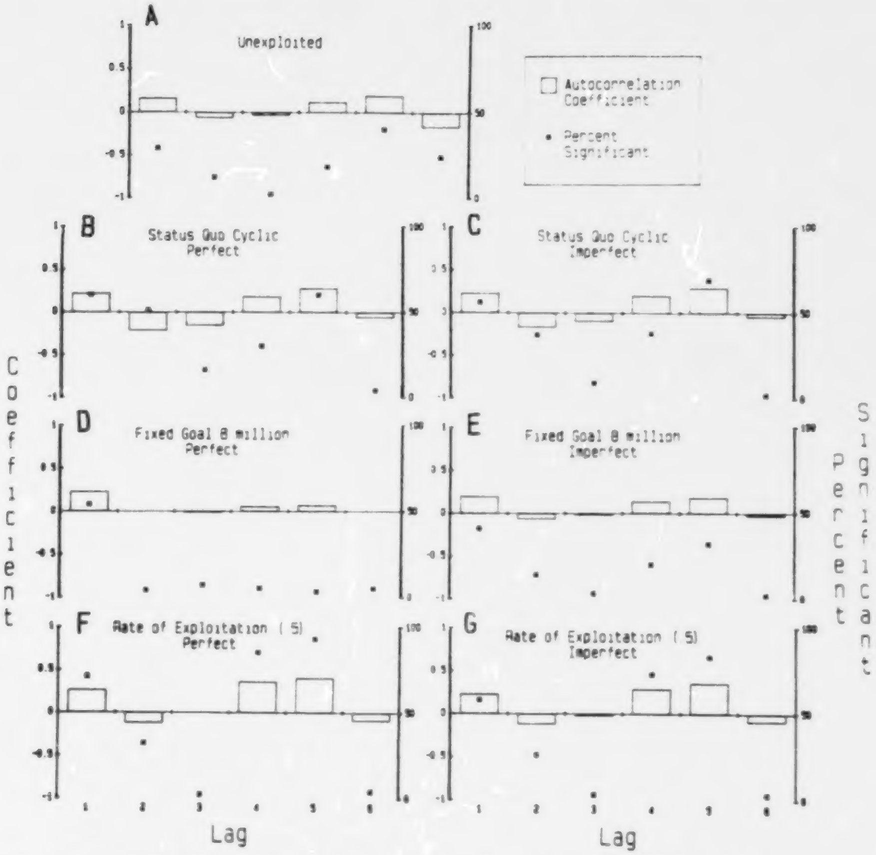

FIG. 23. Estimated autocorrelation coefficients for sample simulations generated by Kvichak simulation model under alternative harvest policies: A. unexploited run, B. status quo, perfect management, C. status quo, imperfect management, D. fixed escapement goal of 8 million, perfect management, E. fixed escapement goal of 8 million, imperfect management, F. fixed fifty percent exploitation rate, perfect management, and G. fixed fifty percent exploitation rate, imperfect management. The autocorrelation coefficient (clear bar) is the mean of 150 coefficients estimated for the respective lag from the 150 sample simulations. Also shown are the percents of the simulations (asterisks) for which the respective coefficients were significant ($P < 0.05$).

were taken from a single, arbitrarily chosen, 106-yr simulation.

The average catch (mean of a 150 mean catches) for the status quo model was 5.32 million per year (Fig. 22C), with a standard deviation of 0.081 million. The observed average annual catch for the Kvichak, 1956–1985, was 5.41 million (Table 3). Simulated runs under the status quo harvest policy generally had a five year cycle. The autocorrelation function estimated for the simulated run time series under status quo management (Fig. 23C) was very similar to that estimated from the historical time series (Fig. 2B). The major difference was that the autocorrelation for lag 1 was more prevalent in the simulated time series than in the observed time series. Cyclic aspects of the simulation results will be discussed further in the next section. In general, the model under status quo management gave an accurate recapitulation of the past Kvichak sockeye population dynamics.

Harvest Policy Evaluation

The model was used to evaluate alternative harvest policies with respect to average catches and cyclic behavior of the simulated runs. In addition to the status quo harvest policy and the unexploited fishery, two broad classes of harvest policies were evaluated.

The first class comprised static harvest policies that did not change from year to year. These included fixed escapement goals wherein the fishery was allowed to harvest fish in excess of the escapement goal, and a fixed rate of exploitation wherein the fishery was allowed to harvest a fixed proportion of the run.

Harvest policies in the second class were dynamic in that they changed from year to year. Because of the large number of possible dynamic harvest policies, we did not attempt an exhaustive evaluation of them. Rather, we examined two types that were reasonable candidates for increasing average catches in view of the implicit spawner recruit submodel. First (hereafter referred to as the cyclic escapement goal policy), we examined a subset of the possible cyclic escapement goal policies in a 5-yr period, where the run was managed for a large escapement goal for 2 yr and for a small escapement goal for 3 yr out of 5. The peak cycle years were staggered so they did not occur on consecutive years. A variety of peak cycle and off-peak cycle escapement goals were examined in the evaluation of this policy.

Second (hereafter referred to as the forecast based harvest policy), we examined a harvest policy conditioned on a preseason forecast of the succeeding year's run. Here, the run was managed for the optimal escapement goal that maximizes current year surplus production, except when the forecasted run for next year was large. If this was the case, then the current year run was managed for a low escapement goal. A variety of low year escapement goals as well as criteria for large runs were examined in the evaluation of the harvest policy.

All harvest policies were examined under both perfect and imperfect management. With perfect management, the escapement goals implicit in the policy were met exactly, provided the run was sufficiently large, otherwise no fishery occurred. With imperfect management, the realized rate of exploitation varied from the target rate of exploitation implicit in the harvest policy based on the random management error implicit in the harvest policy submodel.

UNEXPLOITED RUN

For the case of the unexploited run the average run was 15.77 million. The simulated run was quite variable (Fig. 24), with a low run occurring frequently. The pattern of the simulated unexploited runs was similar to that inferred from the early catches in the Naknek/Kvichak district. There was weak cyclic behavior in the unexploited runs (Fig. 23A).

STATUS QUO HARVEST POLICY

For the case of cyclic escapement goal harvest policy, there was little difference in average catches for the perfect management (5.48 million) and imperfect management (5.32 million) scenarios (Fig. 22C). There was stronger cyclic behavior (i.e., the autocorrelation coefficient was statistically significant ($P<0.05$, Bartlett 1946) in a greater number of the sample simulations) in runs generated under both management scenarios (Fig. 23B and 23C) than in the case of unexploited runs. The sine wave pattern in the coefficients was readily apparent, with a strong autocorrelation for lag of 5 yr, indicative of a 5-yr cycle period. The pattern was much like that observed in the historical time series.

STATIC HARVEST POLICIES

There were only minor differences between average catches for management based on fixed escapement goals (Fig. 22A) and those for cyclic escapement goals. The average catch was greatest (5.4 million) with perfect management and a fixed escapement goal of 8 million. However, there were no statistical differences in average catch among escapement goals from 4 to 12 million with imperfect management and escapement goals from 4 to 8 million with perfect management. There was no cyclic pattern in the runs for the perfect management scenarios (Fig. 23D shows this for the 8 million goal only) and a very weak cyclic pattern for the imperfect management scenario (Fig. 23E).

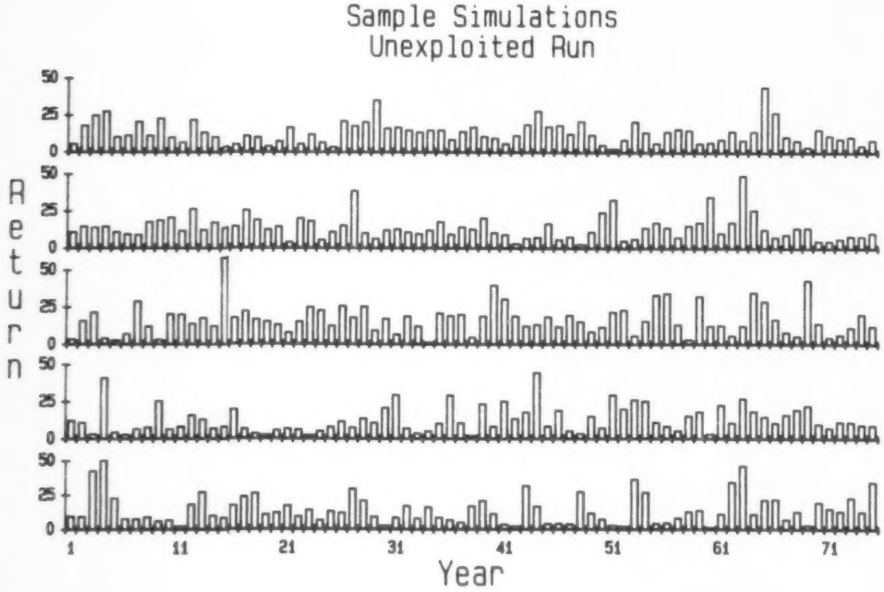

FIG. 24. Simulated time series of annual unexploited runs (millions) based on five arbitrarily selected sample simulations.

There were only minor differences between the average catches for management based on a fixed rate of exploitation (Fig. 22B) and those for a status quo harvest policy. The average catch was greatest (5.21 million) with perfect management and a catch rate of 50% of the run. There were no statistical differences in average catch among the perfect management scenario, U = 50–60%, and the imperfect management scenario, U = 50–70%. There was a strong tendency for returns generated with the fixed rate of exploitation harvest scenario to be cyclic, particularly for moderate (40–50%) rates of exploitation (Fig. 23F and 23G). In fact, the cyclic pattern for fixed rate of exploitation harvest policy was stronger than that for the status quo harvest policy. Under the status quo harvest policy, escapement goals were, in a sense, scaled to the size of the return. The rates of exploitation that actually occurred for the Kvichak averaged 33–42%, except for the post-cycle years, which were higher (Table 3). These rates were very similar to those under a fixed moderate rate of exploitation harvest policy, particularly with management error, thus accounting for the similarity in the cyclic pattern of runs simulated under the two harvest policies.

None of the static harvest policies examined here gave an increase in average catch over that achieved with the status quo harvest policy. In all cases the greatest average catches were 5.2–5.4 million fish, slightly lower than those achieved under the status quo harvest. There was weak cyclic behavior in the unexploited run, indicating some potential for cyclic behavior inherent in the population due to brood year interaction. There was a much stronger cyclic behavior in the run exploited under the status quo and fixed rate of exploitation harvest policies, suggesting that fishing under these harvest policies tended to work in concert with implicit brood year interaction to intensify cyclic behavior of the Kvichak run.

The striking aspect of the results of simulating the Kvichak run under the status quo and static harvest policies was the similarity of catch magnitude and run pattern under a wide variety of harvest policies, as well as the insensitivity of the runs to errors in management. This robustness was unexpected.

The deterministic properties of the spawner-recruit submodel based on the Kvichak data were examined to interpret the above results. Optimal escapement, defined as that which maximizes surplus production for the current brood year, decreases with increasing escapement of the previous brood year, and further, the surplus production a these escapements are the highest for years following low escapement and the lowest for years following high escapements (Fig. 25).

However, this is not a steady-state sustainable surplus production because escapement that optimizes current year surplus production differs, in general, from the escapements in the previous brood year (Fig. 25). If the escapements are constrained to be the same every year (i.e., a static fixed escapement goal harvest policy), then the steady state surplus production is a dome shaped function (Fig. 26) that has a maximum value of 5.95 million for a static escapement goal of 5 million fish every year. This function is very flat, which suggests that there would be little difference in surplus production for static escapement goals between approximately 4 and 8 million (Fig. 26). These results are consistent with those of the simulated average catches under static fixed escapement goal harvest policy. The equilibrium population size is approximately 15 million fish, and consistent with the simulated average runs in the unexploited scenario.

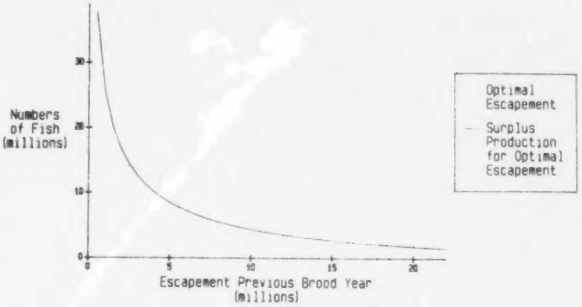

FIG. 25. Escapement that maximizes (dotted line) surplus production for a current brood year, and surplus production (solid line) for the current brood year under the respective optimal escapement plotted against escapement the previous brood year. Values based on deterministic spawner recruit submodel (eq. 1 in text).

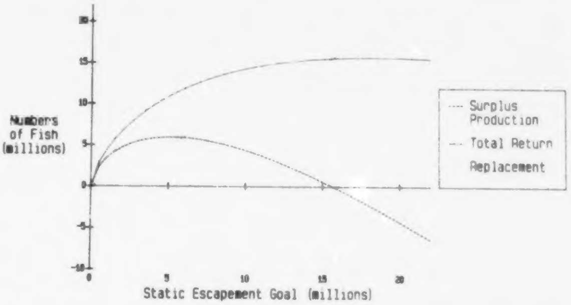

FIG. 26. Total return (solid line), surplus production (dotted line), and replacement escapement (dashed line) plotted against static escapement goal. Values based on deterministic spawner recruit submodel (eq. 1 in text) constrained by constant levels of escapement.

The annual surplus production under the optimal static harvest policy (Fig. 26) is several times less than that which is possible following years of low escapement (Fig. 25). Although it is not possible to maintain this high production every year, it may be possible to increase production over that achieved with static harvest policies by some sort of cyclic escapement goal harvest policy which takes advantage of the high surplus productions available from large escapements immediately following brood years of low escapements (Fig. 26).

If the Kvichak population had a pink salmon life history with a 2 year age at maturity and completely segregated brood lines, then a simple two year cyclic harvest policy could be sustained where one brood (off-peak cycle) line is managed for a fixed low escapement goal and the other brood (peak cycle) line managed for the optimal escapement for the peak cycle based on the escapement achieved in the preceding brood year. Average annual surplus production for the two brood lines was calculated for this idealized situation

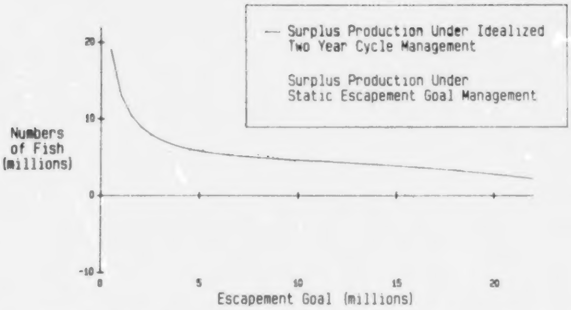

FIG. 27. Sustained surplus production under idealized two years cycle management (see text for details) where abscissa reflects the pre-peak cycle escapement goal (solid line), and sustainable surplus production under static escapement goal management (dotted line), plotted against the escapement goal. Values based on deterministic spawner-recruit submodel (eq. 1 in text).

(Fig. 27) and was found to increase rapidly as the escapement for the off-peak cycle brood line decreased. The surplus production was much greater for off-peak cycle escapement goals less than five million than was possible with static harvest policy. This indicated that some potential exists for increasing catches by adopting low escapement goals for years preceding peak cycle runs.

Unfortunately, with the predominantly 5 yr age of maturity observed for Kvichak sockeye salmon, the return would not be in phase with two year cyclic escapement goals. There would be a high potential for overfishing the cycle brood line without some ability to "tune" the harvest policy so that it could be phased with the variable age at return observed for Kvichak sockeye.

DYNAMIC HARVEST POLICIES

The above analysis of the deterministic properties of the Kvichak spawner-recruit submodel showed that potential increases in average catches may be achieved by adopting dynamic escapement goals. In the cyclic escapement goal policy we chose a five consecutive year sequence of peak (P), off-peak (O), peak, off-peak, off-peak year escapement goals. This cycle of escapement goals would, in general, not be in phase with the year of return for the various peak-cycle lines. In order to synchronize the harvest policy with the runs, we generalized the decision rule for cycle year changes used in simulation of the status quo harvest policy. Here we established a sequence of peak cycle and off-peak cycle years with the above 2 peak/3 off-peak periodicity implicit, by which future runs are managed for peak and off-peak cycle escapement goals. Whenever a peak-cycle run year occurred, the following was done: first, the predominant age of the return was established for the current cycle year (i.e., either 4 or 5 yr depending on the freshwater age of the return); if the predominant year of return for the current cycle year did not correspond to a peak-cycle year in the future sequence of cycle years, then the sequence (i.e., P–O–P–O–O– etc.) was re-initiated at the predominant year of return for the current cycle year, otherwise the sequence of future cycle years was unchanged. In this way the cycle of escapement goals could be kept in phase with the cycle of runs resulting from the cyclic escapement goal policy.

We simulated the Kvichak run for a spectrum of escapement goals. To limit the set of possible escapement goals we assumed that the two peak-cycle and three off-peak cycle goals were the same and between 6 and 24, and 0.5 and 4 million, respectively. Average catches, in both the perfect (Fig. 28) and imperfect (Fig. 29) management scenarios, were highest for off-peak cycle escapement goals less than 1 million and peak cycle escapement goals of 12–20 million.

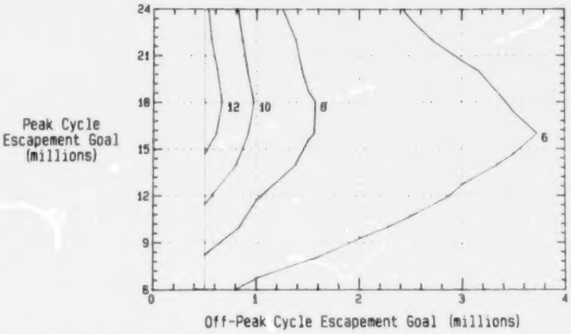

FIG. 28. Average catch (see text for definition of average) in simulated Kvichak runs, managed under cyclic escapement goals harvest policy, plotted against alternative escapement goals for peak cycle and off-peak cycle, for perfect management.

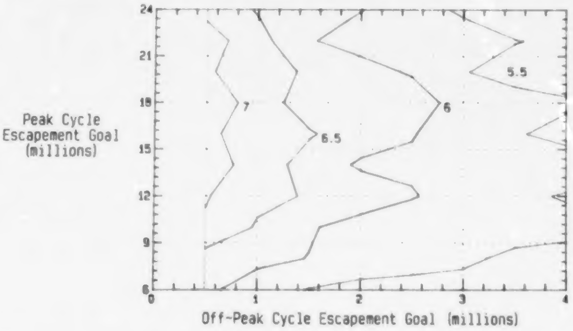

FIG. 29. Average catch (see text for definition of average) in simulated Kvichak runs, managed under cyclic escapement goals harvest policy, plotted against alternative escapement goals for peak cycle and off-peak cycle, for imperfect management.

The average catches in the perfect management scenario were substantially greater than the those under the status quo harvest policy. The average catches under the imperfect management scenario were higher than those under the status quo harvest policy, but much lower than under perfect management. Simulated catches under imperfect management were quite variable with the simulated response of average catch to various combinations of off-peak and peak cycle escapement goals being very irregular (Fig. 29).

We set the forecast-based harvest policy escapement goals on the escapement of the previous year and the forecasted run strength for the next year, so that a sequence of large escapements following small escapement was achieved. For each year two decisions were possible, either an arbitrarily low off-peak cycle escapement goal, or the escapement that maximised current year surplus production. The latter depended on escapement realized in the previous year and would, in general, be large, particularly following small escapements. The following decision rule was used to choose between these alternatives. If the run were forecast to be large the next year, then the off-peak cycle goal was selected. If next year's run were forecast to be weak, then the optimal escapement goal was selected. The only exception to this rule was when the off-peak escapement goal had been selected in the previous year and the run for the current year was expected to be strong. In that event, the optimal escapement was selected even though the outlook was good for a strong run in the following year. Intuitively, it was less risky to obtain the peak cycle escapement from the current year than to harvest the large current year run at a high exploitation rate and rely on the succeeding run, which might not materialize, for the peak cycle escapement.

In the simulation, the forecasted run strength was based on the observed error in ADFG's pre-season Bristol Bay Forecast (Fried and Yuen 1987). Here, the forecast error (F) was expressed as a percentage of the actual run (RN) and assumed to have a normal distribution with mean = 21% and standard deviation = 31%. The forecasted run (R_{hat}) was taken to be:

$$R_{\text{hat}} = (1 - F)\ RN$$

The average catches for the forecast-based harvest policy were simulated for a spectrum of off-peak cycle escapement goals (Fig. 30). A "large" run was taken to be any run with greater than 10 million fish. This criterion was arbitrarily chosen, but results were not sensitive to choice of run size, provided it was above 8 million fish.

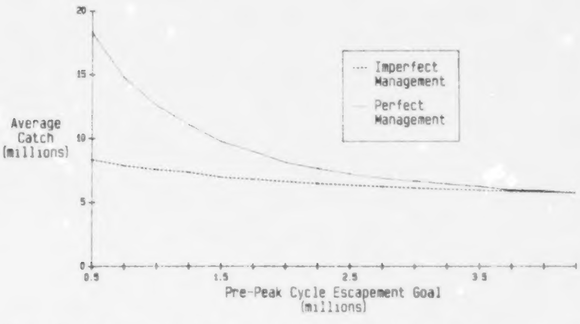

FIG. 30. Average catch (see text for definition of average) in simulated Kvichak runs, managed under forecast-based harvest policy, plotted against pre-peak escapement goal, for perfect management (solid line) and imperfect management (dashed line).

The catches increased with decreasing escapement for the off-peak cycle year. Catches were much larger than those under the status quo harvest policy provided the off-peak goal was less than 4 million fish. The catches under the forecast-based harvest policy were greater than those under the cyclic escapement goal policy. The catches were much larger for the perfect management scenario than for the imperfect management scenario (Fig. 30). This result was similar to that observed for the cyclic escapement goal policy and indicated that careful management would be required to increase yields above those obtained under status quo harvest policy.

Discussion

These analyses have suggested that the cycle of runs of sockeye to the Kvichak has resulted from weak inherent cyclic tendencies intensified by depensatory fishing. The inherent cyclic tendencies were due to interaction between peak- and post-peak cycle brood years, and were weak because of highly variable production as well highly variable age at maturity for which freshwater age has a substantial environmental component.

The simulated catches and cyclic pattern of the runs were extremely similar and consistent among the status quo and various static harvest policies examined. This insensitivity to management policy was due to a flat deterministic relationship between surplus production and static escapement goals and static rates of exploitation. Also, simulated catches under status quo and static harvest policies were insensitive to management error. Under status quo policy and imperfect management scenarios, there was a higher frequency of low escapement brood years. Although production was lower for these low escapement brood years, it was offset by the increased production from succeeding brood years.

Substantial increases in yield could, in theory, be realized with a dynamic harvest policy that attempts to obtain alternating years of relative large and relatively small escapements. Such policy attempts to minimize depressed production in large escapement brood years due to large escapements in the previous brood years. But it would have an inherent two year periodicity and, therefore, would be out of phase with the resulting runs because of the predominant 5 yr age of maturity observed for Kvichak sockeye.

In the cyclic escapement goal policy we examined a modification of the status quo harvest policy wherein the escapement goal in pre-peak cycle years was reduced and an additional peak cycle run was established. In forecast-based harvest policy, escapements alternated between a low pre-peak cycle goal and a high peak cycle goal, based on the forecasted strength for the next year's run. The cyclic escapement policy was phased to the actual cycle of runs by the freshwater age composition of the returns from the last cycle brood year. The forecast based policy was phased according to the forecasted strength of the following year's run.

ADFG (Bue 1986) routinely monitors the magnitude and age composition of Kvichak smolt outmigration. These data provide estimates of the freshwater age composition of the previous cycle return and the most reliable forecast (Fried and Yuen 1987) of the succeeding year's run. Since the data are available 2 yr prior to the current fishing season, phasing of both dynamic harvest policies examined here could be accomplished with the current ADFG program. The results of our simulation study suggested that annual catches may be increased by several million fish with either of the above dynamic harvest policies.

These results depended heavily on the estimated spawner-recruit submodel. Several problems associated with escapement return data may lead to biased estimates of spawner-recruit relationship and have been identified by other researchers. They are: (1) data from heavily fished stocks give underestimates of MSY level escapements (Walters 1981); (2) errors in the measurement of escapement and return, in most cases, give underestimates of MSY level escapement (Walters and Ludwig 1981; Ludwig and Walters 1981); (3) autocorrelation existing in the time series of residuals may lead to biased estimates of MSY level escapement (Glasby 1980); and (4) correlation between residuals and subsequent levels of return may lead to underestimates of MSY level escapement (Walters 1985).

There was no significant autocorrelation in time series of residuals from the spawner-recruit submodel and, further, the residuals were not correlated with subsequent returns. Consequently, we feel that no bias due to factors identified by Glasby (1980) and Walters (1985) existed in the estimated spawner-recruit submodel used here.

The abundance of the Kvichak sockeye had been substantially altered by fisheries exploitation before accurate stock monitoring programs were in place. However, because of the cyclic nature of this run, there has been a wide variety of escapement magnitudes for which returns have been measured. Further, based on the historical record and the consistent behavior of simulated runs, there is nothing to suggest that past escapements since the fishery was established were outside the range of data used to estimate the spawner-recruit submodel. We feel that the data reflect the Kvichak production likely to occur under future harvest levels.

There are certain inaccuracies in the Kvichak data base that could potentially lead to biased estimates of production. We feel that escapements estimated by visual counting from towers were accurate since one sixth of the space time window was actually counted. There may be more variability in the estimates for large escapements due to difficulty in counting the large numbers of fish moving past the tower. Catch estimates were less variable than escapement estimates because they were estimated from sales receipts that reflected the basis of payment for delivered catches. The major source of error has been in allocating catches to river systems, but these are significant only for years of low Kvichak returns; these brood years were excluded in estimating the spawner-recruit submodel. We feel that the magnitude of errors in the Kvichak escapement return data base are not great enough to have caused biases of the magnitude identified by Walters and Ludwig (1981).

In general, the spawner-recruit submodel used in the analysis of the Kvichak cycle was unbiased and reflected the production expected within the error bounds, for the levels of escapement realized under the alternative harvest policies examined. In the estimated spawner-recruit submodel, surplus production increases without limit as the escapement in the preceding brood year approaches zero. Consequently, the minimum pre-peak cycle escapement goal of the MSY harvest policy would occur at the minimum off-peak cycle escapement goal in the set of admissible policies. It is not possible mathematically to define a MSY harvest policy, since it would occur at the boundary of the set of admissible harvest policies. These boundaries reflect the limits of past data, and escapement goals less than these ranges would not be viable because of uncertain production and high risk.

The simulation study showed that catches can be increased in any run having a pre-peak escapement goal below 4 million. These are well above minimum escapement levels observed in the past. We advocate the establishment of a second cycle run, returning 2–3 yr later or earlier than the present cycle run, and recommend that the escapement goal in the year prior to these cycle years be set at 1–2 million.

There are certain problems associated with the implementation of dynamic harvest policies. First, the current mid-cycle run is very low, and rebuilding this to peak-cycle levels will be very difficult in view of the need to intercept some Kvichak fish in order to harvest the other eastside sockeye stocks. Second, the dynamic harvest policy must be continuously phased with the cycles of resulting runs. At present there is a single peak cycle run, and great care must be taken to maintain it. The forecast-based harvest policy gave the highest average catches and, further, there is less risk in overharvesting the peak cycle run forecasted to occur the following year. The pre-season forecast has been very accurate in determining the year of peak-cycle run, but quite variable in predicting absolute run magnitude (Fried and Yuen 1987). The simulation study demonstrated that increased yields under dynamic harvest policies occurred despite the reality of forecast errors, since these were considered in the simulations.

Stocks exploited together and at equal exploitation rates cannot be managed for stock specific escapement goals. Paulik et al. (1967) and Ricker (1958) have suggested that the rate should reflect the equilibrium MSY escapement level based on the pooled stocks escapement/return relationship. Hilborn (1976) later re-examined the mixed stocks harvest problem using stochastic dynamic programming which allowed for rates of exploitation conditioned on relative run strength of constituent stocks. Hilborn's analysis showed that optimal rate of exploitation, in parameter combinations examined, was lower than that based on fixed pooled stock escapement (Paulik et al. 1967) when the abundance of one or more stocks was depressed relative to the others commonly exploited.

Realized catches will be less under mixed stock fishing constraints than for stock specific fishing. This follows from Ricker's (1958) conclusion that managing for fixed escapement goals under realities of year-to-year variation in return resulted in greater catches than managing for fixed rate of exploitation at equilibrium MSY. Because of this, any means of achieving more stock specific harvests, such as time area closures, and/or reallocating interception fisheries to more terminal areas will increase yields (Paulik et al. 1967). With stock specific management techniques it is possible to increase yields above those with the fixed rate of exploitation dictated by mixed stocks fisheries. The marginal increase in yield due to stock specific management can be used to justify the cost of those programs.

These theoretical results were obtained from the simple compensatory stock-recruitment model, but would also apply to the spawner-recruit submodel with brood year interaction developed here. In the Kvichak model, increased catches were possible only with the establishment of a second peak cycle run, as evidenced by the similarity of catches under the status quo harvest policy and static harvest policies. To do so requires substantial reductions in exploitation rate on Kvichak fish in some of the mid-cycle runs.

The Kvichak return is harvested simultaneously with the Naknek and Branch River stocks. The Naknek returns are currently much greater than MSY level escapement. Thus, any drastic curtailment of fishing in the Naknek/Kvichak district to increase off-cycle Kvichak escapement will result in significant over-escapement to the Naknek River system. There exists some spatial separation in the Kvichak and Naknek run but it varies in magnitude among years. The extent of the seasonal divergence in stock specific exploitation rates can be estimated in-season, because in most years, the Naknek run has a higher proportion of age .3 fish than does the Kvichak. Simple linear programming methods with real time catch and escapement age sampling can be used to estimate instantaneous stock specific exploitation rates. Scale pattern analyses can also be used to estimate stock specific rates of exploitation in season (Marshall et al. 1987). In theory, it would be possible to evaluate alternative in-season harvest policy ranging from full Naknek/Kvichak District openings to very restrictive openings in special harvest areas inside the Naknek River.

Finally, this paper has identified several tangible (in terms of increased yields) benefits of intense fisheries management and research. If exploited salmon stocks are to be maintained, it is vital to develop and implement more accurate stock assessment programs including catch and escapement enumeration, age composition sampling, and catch allocation. Harvest policies are always hampered by insufficient information as the fishery is developed. Fisheries management is an adaptive process (Walters and Hilborn 1976, 1978), and knowledge of the response of the populations to the fishery is essential to adaptive fisheries management.

Acknowledgements

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In-Season Management of Fraser River Sockeye Salmon (*Oncorhynchus nerka*): Meeting Multiple Objectives

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Abstract

WOODEY, J. C. 1987. In-season management of Fraser River sockeye salmon (*Oncorhynchus nerka*): meeting multiple objectives, p. 367–374. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Management of Fraser River sockeye stocks was based upon annual achievement of (a) escapement goals which reflected stock rebuilding and optimum escapement objectives and (b) allocation of the catch as provided by terms of the Sockeye Salmon Fisheries Convention. In-season data collection was designed to provide the International Pacific Salmon Fisheries Commission with information necessary for decision-making on a real-time basis to achieve both catch and escapement objectives by stock. Needed were assessments of annual run strengths, timing, and migration routes. Data collection included real-time estimates of commercial catch; acoustic estimation of daily escapement; test fishing to provide early indication of timing and abundance; and racial analysis of commercial and test catches. Integration of these data-generating activities in the management process and rapid analysis of the data enabled the Commission to respond on short notice to changes in stock abundance. Modifications to the pre-season fishing plan were based on the need to achieve escapement goals while distributing the catch equally between fishermen of Canada and the United States. Stock rebuilding goals were met for several spawning populations which had been devastated by blockages to migration in the Fraser River and by overfishing. Escapement goals were increased to meet both the stock rebuilding and optimum escapement objectives. Simultaneously, nearly equal catches were taken by fishermen of Canada and the United States in the Convention area during the 39 years of Commission regulatory responsibility (1946–84).

Résumé

WOODEY, J. C. 1987. In-season management of Fraser River sockeye salmon (*Oncorhynchus nerka*): meeting multiple objectives, p. 367–374. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La gestion des stocks de saumon nerka du fleuve Fraser a été fondée sur l'atteinte annuelle a) des objectifs de remonte qui reflétaient les objectifs de remonte optimale et de reconstitution des stocks et b) de l'allocation des prises comme prévu par les dispositions de la Convention des pêches du saumon nerka. La collecte des données pendant la saison de pêche visait à fournir à la Commission internationale des pêches du saumon dans le Pacifique les renseignements nécessaires pour la prise de décision en temps réel pour atteindre les objectifs de capture et de remonte par stock. Il était nécessaire d'évaluer l'importance de la remonte annuelle, le moment du frai et les routes de migration. La collecte des données comportait des estimations en temps réel des prises commerciales, une estimation acoustique de la remonte journalière, une pêche d'essai pour fournir des indications anticipées sur le moment et l'abondance du frai, et une analyse raciale des prises commerciales et d'essai. L'intégration de ces activités génératrices de données au processus de gestion et une analyse rapide des données ont permis à la Commission de réagir dans un court délai aux changements dans l'abondance des stocks. Les modifications apportées au plan de pêche précédant la saison ont été basées sur la nécessité d'atteindre des objectifs de remonte tout en répartissant les prises en parts égales entre les pêcheurs du Canada et des États-Unis. Les objectifs de reconstitution des stocks ont été atteints pour plusieurs populations de géniteurs qui ont été décimées à cause d'obstructions empêchant la migration dans le fleuve Fraser et de la surprêche. On a augmenté les objectifs de remonte pour atteindre aussi bien les objectifs de remonte optimale que ceux de reconstitution des stocks. En même temps, des prises presque égales étaient prélevées par les pêcheurs du Canada et des États-Unis dans le secteur relevant de la Convention au cours des 39 années pendant lesquelles la Commission a été responsable de la réglementation (1946 à 1984).

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Introduction

In-season management of Fraser River sockeye salmon evolved over the 39 years (1946–84) of regulation by the International Pacific Salmon Fisheries Commission (IPSFC) to meet the changing exploitation patterns due to gear improvements and seaward expansion of the fishery. Intensive management was considered necessary to achieve the multiple objectives set forth in the Sockeye Salmon Fisheries Convention. Ratified in 1937, the Convention established the IPSFC for the protection, preservation, and extension of the Fraser River sockeye. Specifically, it was to rehabilitate stocks depleted by periodic in-river passage problems dating back to 1913 and the overfishing which followed (Thompson 1945), and to regulate a progressively more efficient fishing fleet by international control, thereby fostering cooperation within the Convention Area (Fig. 1). Fully developed, the program was an integrated management scheme including pre-season forecasting, computer simulation of the fisheries and in-season regulation. Rapid acquisition and analysis of reliable fishery and biological data were critical for the day by day regulation of the fisheries and to meet the annual catch and escapement goals by stock.

Fraser River sockeye stocks are characterized by moderate to extreme interannual variation on a 4-yr cycle, often with one large (dominant cycle), one moderate (sub-dominant), and two low (off-cycle) production years. This pattern (quadrennial dominance) is primarily the result of 4-yr-old adults reproducing on successive generations (Ward and Larkin 1964). The year-to-year variation in abundance of many stocks results in greatly variable stock complexes on each of the four cycles. Consequently, rebuilding was needed for low production cycles of some stocks while dominant year returns of other stocks were sufficiently large to permit a harvest. In the management of each cycle year, therefore, stock rebuilding and optimal spawning escapement objectives for co-migrating stocks were balanced on the basis of the pre-season forecasts to provide the best mix of harvest and escapement. Hence, foregoing catch or stock rebuilding targets were, necessarily, trade-offs in setting the annual escapement goals.

In-season management required early estimates of abundance, timing of onshore migration, and daily escapement, by stock, for a composite of 6 to 10 major stocks each year. Fraser River sockeye enter coastal fishing areas between late June and early September (see schematic timing curves, Fig. 2). Since individual sockeye migrate through the commercial net fishery areas (see Fig. 1) in about 8 days and the bulk of a stock may pass any point along the migratory route in a period of 15 days, the IPSFC maintained a real-time monitoring of the stocks by means of a 24–48 h turn-around on the collection, processing, and analysis of in-season data. Rapid acquisition of catch and escapement data was particularly important when fine tuning the fishing effort.

Data Collection

Four in-season data collection programs evolved: real-time estimates of catches including catch per unit of effort (CPUE), test fishing CPUE during periods of commercial closures, acoustic monitoring of the escapement, and racial analysis of commercial and net fishing catches by scale analysis.

CATCH ESTIMATION

Catch monitoring during and immediately after each fishing period provided the first estimate of the daily catch

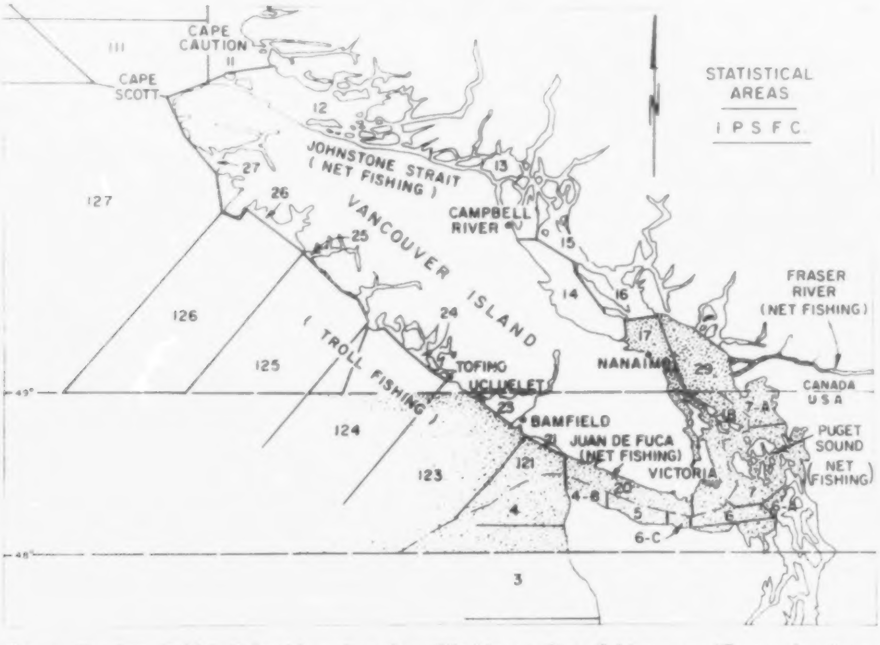

FIG. 1. Southern British Columbia and northern Washington State fishing areas (Convention Area indicated by stipling).

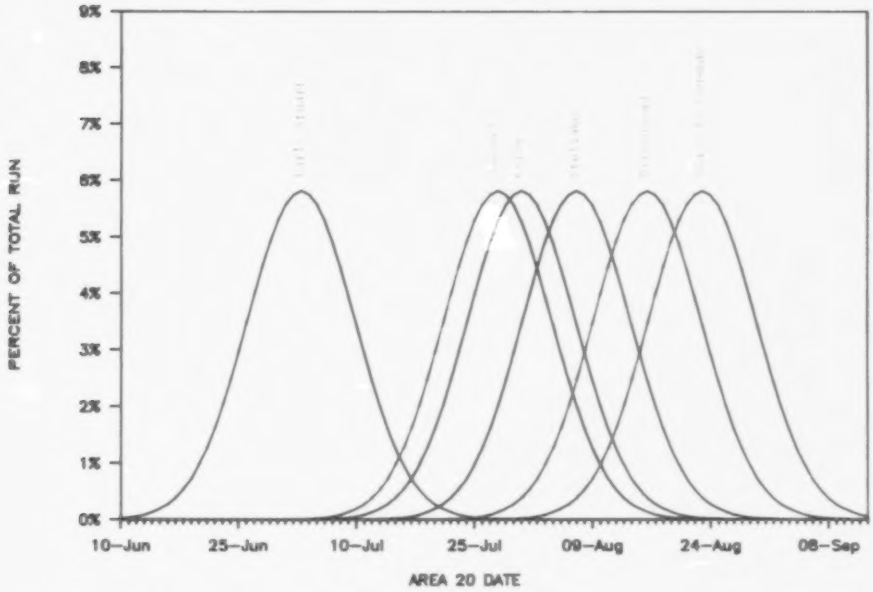

FIG. 2. Schematic timing curves for six major Fraser River sockeye salmon stocks.

by each commercial net fishing fleet (purse seine, gill net, and reef net). Well established communication links between Commission staff and key industry personnel were vital for effective catch monitoring and, as each fishery proceeded, telephone contacts provided the data necessary for a projection of the magnitude of the catch before the fish were landed. Following the daily landings, a telephone survey of major fish buyers gave a sample of catch and CPUE data which, along with aerial gear counts, permitted an updated estimate of catch within 24 h of the completion of daily fishing periods. Alternately, the daily estimate of catch was based upon the proportion of total catch purchased by major fishing companies. Landing information for a few reliable companies was used with prior week purchase data to project catches.

Landings from continuing (as opposed to weekly) fisheries, particularly the Canadian Areas 123–124 troll fishery (Fig. 1), were estimated daily and became the "distant early warning system" of developing runs since these fisheries revealed daily abundance trends several days before the fish arrived in coastal net fisheries.

Final catch estimates were obtained from landings recorded on fish tickets (United States) or dock tallies and fish sales slips (Canada). As the IPSFC mandate applied to a relatively small geographical area, most data could be obtained and entered into computer files within 1 or 2 wk after each fishery. Catch data from Canadian non-Convention areas were obtained weekly from the Department of Fisheries and Oceans, in order to monitor the complete catch of Fraser River sockeye.

Historical daily catch data were available from fish sales slips and could be used to generate past catch records for comparison with current catch and CPUE estimation of run size and timing.

TEST FISHING

Prior to the fishing season and between commercial fishery periods, the Commission operated test fisheries in areas where it was essential to have dependable estimates of run strength and timing. Test fishing was necessarily standardized as to location, time, gear, and effort expended. Three migratory areas were monitored routinely for as many as 30 seasons (Fig. 1): Juan de Fuca Strait (Area 20), Puget Sound (Area 7), and the Fraser River (Area 29). The primary purpose was to monitor the abundance of fish migrating into the Convention Area (e.g., Area 20) or escaping into the river (Area 29). CPUE by the gill net and purse seine test vessels was used in conjunction with historical records to obtain a direct measure of incoming abundance during fishery closures. In the lower Fraser River, test fishing also provided an early estimate of daily escapement (Woodey 1984).

The second major purpose of the test fishery was to provide scale samples and other biological data for racial analysis of the sockeye stocks making up the daily migrations and escapements.

ACOUSTIC MONITORING

Daily escapement of sockeye was acoustically estimated as the fish passed Mission, B.C., the upstream fishing boundary in the Fraser River. A low frequency (50 KHz), dry paper echo sounder with an approximately 43° (full angle) sound cone was used to record the fish targets (sampling accounts for approximately 1.0% of the fish passing upriver). The transducer was mounted in a modified trolling stabilizer and suspended from a vessel davit. Transects at right angles to the river flow at a single site were traversed repeatedly for 14–21 h daily to obtain target density information, i.e., targets per transect for 3 m depth strata. Stationary sounding for one hour in every eight provided echo traces of passing fish. Swimming speeds were determined at each depth stratum and with target density were used to estimate the daily fish population. Since resident fish species were also present, it was necessary to estimate their abundance by obtaining a background target density during periods of low sockeye migration (i.e., immediately after commercial fishing in the lower river). Salmon species composition was estimated from test fishing records.

Generally, more than 10 000 fish per day were needed to obtain reasonable confidence limits around the daily population estimates. However, unbiased estimates, if made daily throughout closed periods, were expected to provide good cumulative estimates of escapement during closures (3–5 days per week) since the random error would be small even with low average daily abundance. Most daily escapements exceeded 10 000 fish and sometimes reached as high as 500 000 fish during the main run periods.

Racial Analysis

Scale analysis provided managers with in-season estimates of racial composition of Fraser River sockeye salmon mixed-stock catches and escapements (Clutter and Whitesel 1956; Henry 1961). Random samples of 120 to 240 sockeye were obtained weekly from as many as 12 commercial fisheries, and daily from 3 test fisheries. Samples were collected from each gear type in multiple gear (purse seine and gill net) fisheries. Test fishery catches were often sampled daily to ensure sufficient scales for analysis, or to monitor rapidly changing stock composition. Purse seine catches were preferred for analysis of racial composition because purse seines are less selective than other gear types. Purse seine catches from Puget Sound were sampled for length, weight, and sex as well as for scales. The total catch by age group and stock was calculated for all gear types and combined to obtain estimates of total runs.

Circuli counts from the lacustrine zone (with and without spring growth), and fish age were determined from each scale. During periods of difficult stock identification, circuli spacing was also measured. Freshwater growth of Fraser River sockeye has been shown (Henry 1961) to be environmentally affected: fish from oligotrophic lakes, or from lakes with high population density grow more slowly and, hence, have fewer circuli. Nevertheless, interannual variation in circuli counts has been substantial and only samples from the same year-class could be compared usefully. Thus, scales from age 3_2 (Gilbert-Rich method of age designation) precocious males or "jacks" of one year were collected from the spawning grounds and circuli counts from these fish were used to analyse mixed stock scale samples of 4_2 adults the following year.

The estimation of racial composition followed the methods of Henry (1961), wherein the frequency distribution of circuli counts in mixed stock samples was compared with the known distributions of discrete contributing stocks. Scale radius measurements and length by sex and age also provided biological information for stock composition determinations. The pre-season forecast of stock abundance, historical arrival timing, and known migrational characteristics of the stocks were used subjectively to identify, by stock, the modal points in the frequency distributions. The in-season analysis was restricted to stocks expected to make a significant contribution to the adult return. This was considered important in achieving high overall accuracy in the stock compositon estimates since inadequate age 3_2 scale samples and shifts in the modal points of adult readings could have led to erroneous identification of contributing stocks. A post-season review and assessment of racial analyses used data from spawning ground samples of all stocks (including minor stocks excluded in-season) and was usually in good agreement with in-season analyses. Prospects for the application of new technology to scale analysis was investigated by Cook and Guthrie (1987).

Data Analysis

In-season analysis of the data collected in the four programs took several forms. These included rigorous statistical treatment, run reconstructions, and historical, and sometimes, intuitive catch analyses. Together they provided the managers with in-season estimates of run size, timing, and migratory behavior and can be subdivided as follows:

1) *Statistical treatment.* Stock sizes were estimated from historical catch and CPUE data, using linear, non-linear, and multiple regression models. Both commercial and test fishery catches were used successfully. For example, the numbers of Adams River sockeye passing through Juan de Fuca Strait were estimated from the maximum Area 20 purse seine CPUE on two consecutive days (Fig. 3). As Fraser River sockeye also migrate to the river via Johnstone Strait (Fig. 1), estimates of northern route abundance were derived in a similar manner, but using Area 12 and 13 CPUE.
2) *Reconstructions.* Daily run estimates were calculated by first aligning catches in different areas and times according to known travel time between respective fishing areas and Mission, B.C. Catches thus summed were then added to the daily Mission escapement estimates obtained by acoustic monitoring. This yielded an estimate of the unfished daily abundance at one (hypothetical) point. Calculated trends in daily abundance gave an up-to-date evaluation of the run progress, particularly for summer-run sockeye, i.e., stocks which tend not to delay in the estuary but proceed directly up the Fraser River. These evaluations were also used to estimate times of peak abundance (used for run peak CPUE analyses), determine exploitation rates, and project future catch and escapement. The reconstructed daily run size was also compared to historical and theoretical (normal distribution) models of abundance. Before the peak of the run, both the projected day of peak migration and the run size were varied in the models to predict daily cumulative abundances which were then regressed against observed data. Estimates of run size and timing were obtained simultaneously by minimizing unaccounted variance.
3) *Catch analysis.* Establishing the time of peak occurrence of stocks in distant fisheries was particularly valuable for forecasting run timing and day by day abundance in the major local net fisheries. The troll fishery, located 3 to 10 days migration time seaward of the first net fisheries,

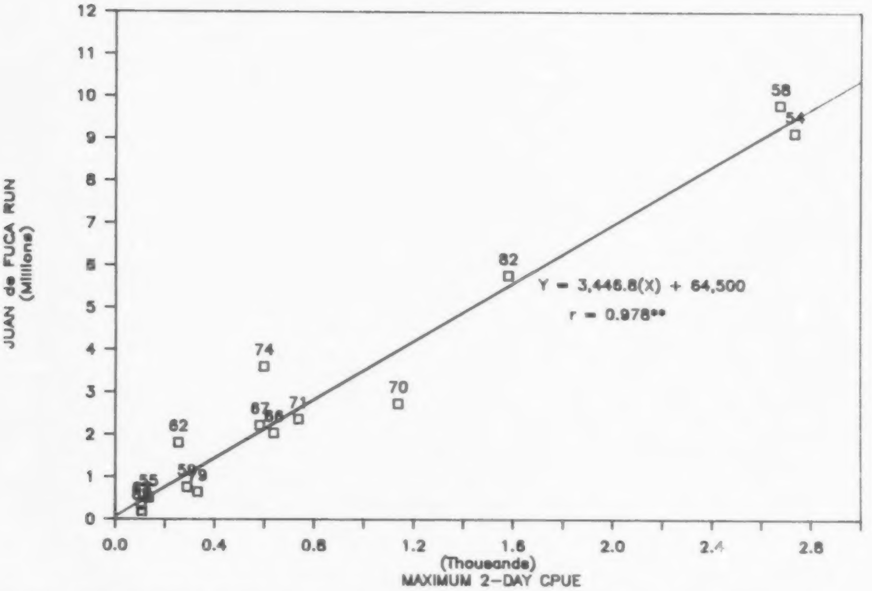

FIG. 3. Relationship between abundance of Adams River sockeye salmon migrating via Juan de Fuca Strait and maximum 2-day catch per purse seine in Area 20.

played an important role in providing an initial source of such data. Analysis of in-season data also benefited from certain intangibles, particularly the comments of fishermen on fish behavior, e.g., depth and rate of travel, that could affect exploitation rate. However, an experienced observer was required to properly interpret such qualitative data. Often several differing estimates for each migration parameter were obtained for both objective and subjective analyses and these had to be rationalized and interpreted by the staff.

Decision-Making

The Commission usually met twice weekly to evaluate the analyses of data on sockeye migration and abundance and decide on in-season adjustments to fishing regulations. Weekly catches were made in the four major Convention Area fisheries (Canadian troll, Area 20, Area 29, and United States Puget Sound) and two major non-Convention areas, and rapid evaluation was required to permit decisions affecting current and following week fishing times. By maintaining rapid data flow and analysis, the Commission was able to make decisions on adjustments through the season that were necessary to achieve the multiple objectives of the Convention. Those decisions usually depended upon escapement and catch allocation requirements.

Escapement goals were achieved on a stock by stock basis. Fortunately, peak onshore arrival timing differs among stocks and permits several stocks, or groups of stocks to be sequentially managed. Significantly, the escapement goals often dictated that the management plan achieve large differences in the exploitation rates for some stocks and fishing regulations were drafted with this in mind. Compromises between differing escapement requirements of co-migrating stocks were always made with a view to the long-term goals of stock rebuilding and optimum escapement, while keeping in mind the economic importance of annual harvests by dependent fleets. At times, the pre-season escapement goals were adjusted upwards during the fishing season to obtain more spawners for needy stocks when larger actual returns of these permitted a revision. Such decisions were based on results of in-season analysis of abundance and the relative abundance and timing of co-migrating stocks.

Differing behavioral characteristics of the stocks were also utilized to alter harvest rates. Pre-riverine migration delay caused late-run (delaying) stocks to be separated in time from summer-run (non-delaying) stocks in the Fraser River and this allowed different rates of exploitation. In certain cases, fish quality considerations determined the exploitation pattern (i.e., where fishing was allowed) since large price reductions accompanied the progressive maturation of delaying stocks. In general, the Fraser River (Area 29) fishery was directed at non-delaying stocks while delaying stocks were fished in marine migratory areas where quality was high.

Results

STOCK REBUILDING

Of the objectives set forth in the 1937 Convention, stock rebuilding was well achieved. Certain stocks were particularly devastated by blockages to migration in the Fraser River at Hell's Gate (Thompson 1945). Foremost of these were the Horsefly River and associated Quesnel Lake watershed stocks. Subsequent overfishing further depleted these stocks such that insignificant returns occurred on one cycle year and none occurred on off-cycle years. Time and area closures after construction of the Hell's Gate fishways boosted the Quesnel area escapement from 1 000 spawners in 1941 to 110 000 in 1953 (Fig. 4). Recent management strategies called for accelerated escapement rehabilitation (IPSFC 1982). For instance, in 1985, the pre-season escapement goal of one

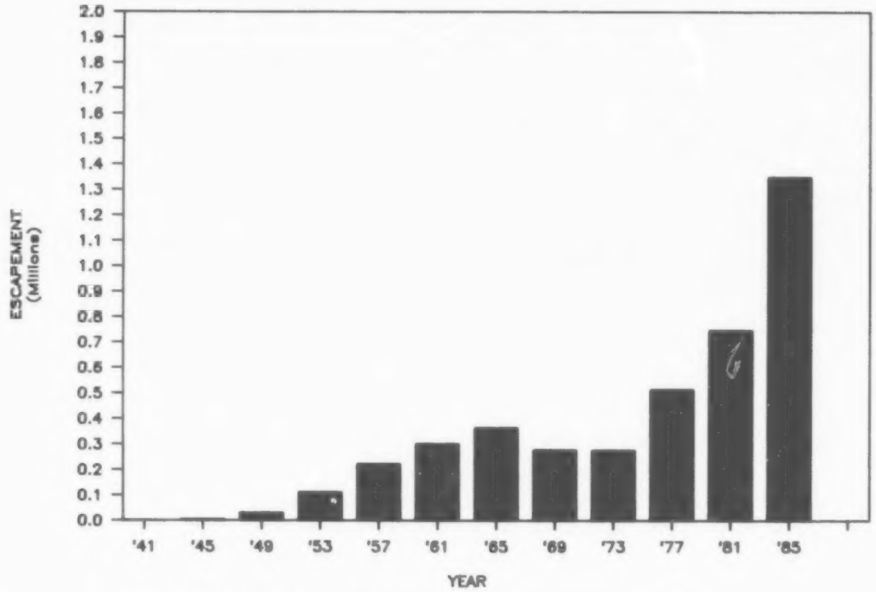

FIG. 4. Quesnel area sockeye salmon escapements, 1941–85.

million was adjusted during the season to respond to a larger-than-forecast return, and an escapement of 1.35 million Quesnel area spawners was achieved. The total return of these stocks in 1985 was estimated at 9.5 million which provided a commercial catch of nearly 8.0 million sockeye with a landed value of $ 75 million (Can.).

Lower Shuswap River sockeye were also managed for stock rebuilding. From levels of 9 000–31 000 spawners on the dominant cycle (1950, 1954, etc.) in the period 1950 to 1970, it was possible to increase the escapement to 514 000 spawners in 1982 (IPSFC 1983). By employing stock rebuilding strategies, the Commission has also achieved healthy sockeye populations in several other streams where depletion was formerly evident. There was continued effort to rebuild formerly productive stocks which were devastated by fish passage problems and overfishing and to increase non-dominant cycle runs of strongly dominant stocks. In addition, spawning channels were constructed at four locations in the Fraser watershed to mitigate local environmental deterioration (Cooper 1977) although these accounted for only 6.4% of Fraser River sockeye production from 1977 to 1984 (i.e., 3 664 000 fish).

TABLE 1. Comparison of pre-season adult sockeye salmon escapement goal and escapement obtained.

	Pre-season goal	Actual escapement	% Deviation
1974	2 400 000	1 657 000	−31 %
1975	950 000	921 000	− 3 %
1976	900 000	781 000	−13 %
1977	1 500 000	1 014 000	−32 %
1978	2 650 000[a]	2 485 000	− 6 %
1979	1 200 000	1 368 000	+14 %
1980	1 000 000	830 000	−17 %
1981	1 700 000[a]	1 384 000	−19 %
1982	3 100 000	4 008 000	+29 %
1983	1 500 000	965 000	−36 %
1984	870 000	922 000	+ 6 %
1985	2 300 000[a]	2 140 000	− 7 %
Means	1 673 000	1 540 000	− 9.6%[b]

[a] Pre-season goals based on annual forecast adjusted during the fishing season as actual returns materialized.

[b] Mean of annual values.

ANNUAL ESCAPEMENTS

Annual escapement goals for each stock were premised on rebuilding needs and estimated optimum escapements for each cycle year. The mix of major and minor stocks varied greatly from cycle to cycle and, therefore, total escapement goals changed every year. However, regardless of the cycle, attainment of spawning escapement was considered the best measure of the short-term success of the fishery management strategy. Comparison of the 1974 to 1985 goals with the escapements actually obtained (Table 1) suggested that the management program tended to attain escapements in the order of 10% below the annual goals. However, actual annual escapements increased 30% in each 4-yr period between 1974–77 and 1982–85 and resulted in a rise in mean annual production (Fig. 5). Stock rebuilding is important in the interpretation of these data, as without the large returns of several rebuilt stocks a lower plateau of production may have occurred.

CATCH ALLOCATION

The international catch allocation objective of the in-season management of Fraser River sockeye by the Commission pertained to the Convention Area alone. Achieving a balance in Canadian and United States catches each year was troublesome owing to the difficulty of predicting fishing ef-

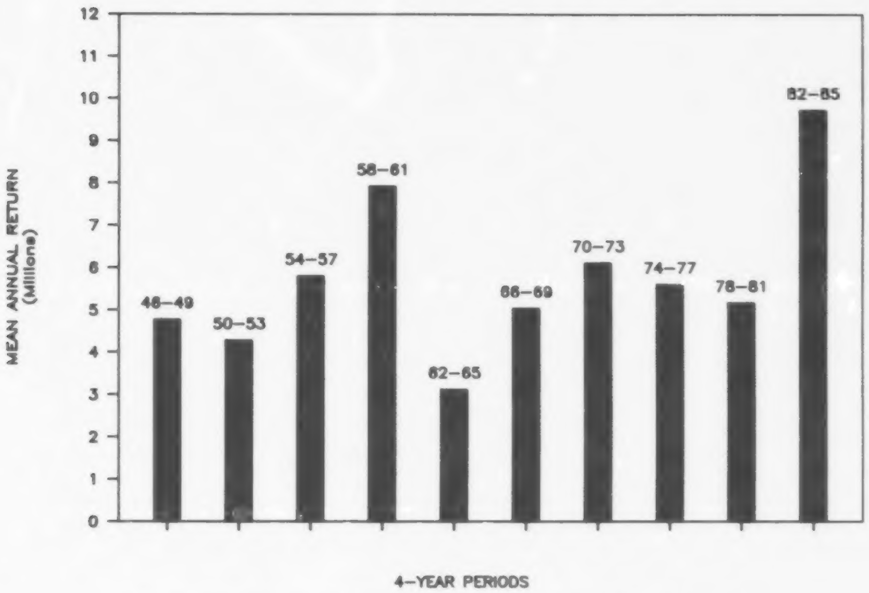

FIG. 5. Average annual (4 yr) Fraser River sockeye salmon returns.

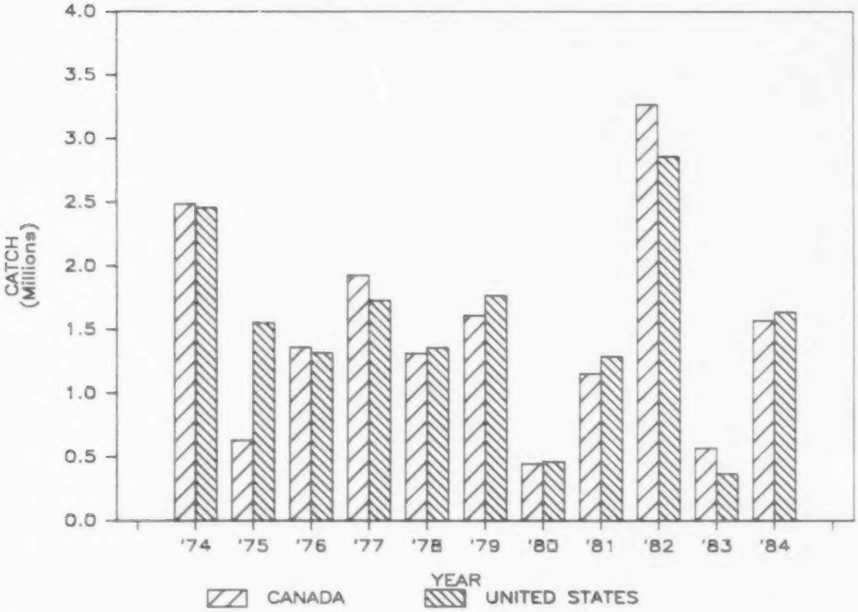

FIG. 6. Annual United States and Canada catches of sockeye salmon in Convention Area fisheries, 1974–84.

fort and fleet efficiency and estimating run sizes. In addition, fishing industry strikes led to severely unbalanced catches in some years (e.g., 1975; Fig. 6). Nevertheless, the long-term allocation objective was largely met over the 39 years of regulatory responsibility (1946–84). Total landings in the period were: Canada — 62 909 000 sockeye (49.69%) and United States — 63 683 000 (50.31%).

Increased interceptions by Canada outside the Convention Area (IPSFC 1984) became important in the latter years of Commission regulation. These catches reduced the number of sockeye which were subsequently available in the Convention Area and were important when the countries were redefining catch allocation objectives under the new Pacific Salmon Treaty, signed in 1985. Implementation of the new Treaty by the existing IPSFC in 1985 created special difficulties, first, because catches of Fraser River sockeye in all areas were to be included in the allocation computations and, second, because of the need to allocate to gear type in Canadian waters. However, attainment of these redefined goals was possible because the existing management procedures enabled close monitoring of catches and escapements as well as in-season analysis of stock size and behavior with which to make regulatory decisions.

The cooperative spirit between the United States and Canada, the achievements of dedicated scientists and managers and the action of the IPSFC over 39 years led to the fulfillment of the objectives and purpose of the Convention.

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Evidence Against the Existence of Cyclic Dominance in Fraser River Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

WALTERS, C. J., AND M. J. STALEY. 1987. Evidence against the existence of cyclic dominance in Fraser River sockeye salmon (*Oncorhynchus nerka*), p. 375–384. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Estimates of spawning stock sizes and subsequent recruitment for eight Fraser River stocks do not support the hypothesis that offcycle runs are less productive, or have lower equilibrium stock sizes, than dominant cycle year runs. Differences that have been estimated by fitting recruitment curves using regression methods are likely due to biases in applying the regression methods to the short time series that are available for the individual cycle years; such series are not expected to be representative due to oversampling of high productivities at below average stock sizes and low productivities at above average stock sizes. No significant autocorrelation or cyclic pattern is evident in the residuals from aggregate recruitment curves fitted to all cycle years for each stock, and there does not appear to be any changing environmental effect that is shared by all the stocks (no shared residual effects that are correlated over time). However, there do appear to be significant negative interactions among cycle years for some stocks, such that increasing abundance in one cycle year is correlated with reduced productivity in the other cycle years. Cyclic abundances now appear to be maintained largely by high fishing rates, and it is possible that aboriginal fisheries were responsible for establishment of the cyclic patterns that have been inferred from historical records. By lowering exploitation rates on all stocks in all cycle years, it should be possible to substantially increase the value of the fishery even if some very weak offcycle runs never recover.

Résumé

WALTERS, C. J., AND M. J. STALEY. 1987. Evidence against the existence of cyclic dominance in Fraser River sockeye salmon (*Oncorhynchus nerka*), p. 375–384. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Des estimations de la taille du stock de géniteurs et du recrutement effectuées pour huit stocks du fleuve Fraser n'appuient pas l'hypothèse voulant que les remontées acycliques soient moins productives ou présentent des tailles de stock à l'équilibre moins importantes que les remontées des années cycliques dominantes. Les écarts qui ont été estimés par ajustement des courbes de recrutement à l'aide de méthodes de régression découlent probablement de biais dus à l'application des méthodes de régression aux séries chronologiques très courtes dont nous disposons pour les années cycliques individuelles. On ne peut s'attendre à ce que de telles séries soient représentatives étant donné le suréchantillonnage des productivités élevées des stocks de taille inférieure à la moyenne et des faibles productivités des stocks de taille supérieure à la moyenne. On ne note aucune autocorrélation ou allure cyclique significative pour les résidus des courbes de recrutement regroupées ajustées à toutes les années cycliques de chaque stock et il ne semble pas y avoir d'effet environnemental variable commun à tous les stocks (absence d'effets résiduels communs corrélés en fonction du temps). Il semble cependant y avoir pour certains stocks des interactions négatives significatives entre les années du cycle, de sorte que l'augmentation de l'abondance au cours d'une année est corrélée avec une réduction de la productivité au cours des autres années du cycle. Les abondances cycliques sont en grande partie maintenues par les taux de pêche élevée et il est possible que les pêches autochtones soient à l'origine des cycles qui ont été déduits à partir de données historiques. Il devrait être possible, en abaissant les taux d'exploitation de tous les stocks au cours de toutes les années, d'accroitre de façon appréciable la valeur de la pêche même si certaines remontées acycliques très faibles devaient disparaître.

Introduction

One of the most striking phenomena in the population dynamics of Pacific salmon is the cyclic variation in sockeye run sizes to the Fraser River. According to Ward and Larkin (1964), dominant runs occurred throughout the 19th century on what is now called the "1905 cycle year" in the 4-yr cycle. Following a major blockage of the Fraser River at Hells Gate in 1913, the early dominance pattern was destroyed, and several stocks later reestablished dominance patterns but not on the same cycle year; the largest total runs in recent years have been on the new dominant cycle year (1906) for the Late Shuswap (Lower Adams River) stock. Current cycle patterns, run timings, and other stock characteristics are reviewed in Vernon (1982).

Ward and Larkin (1964) and Larkin (1971) argued that cyclic dominance may result from the depensatory effects of predators such as trout and squawfish. They proposed that interactions between the cycle years (strong get stronger, weak get weaker) may occur through depensatory predation moderated by "buffering" from the effects of predation on juveniles of one cycle year by juveniles of another cycle year. Support for the Ward–Larkin hypothesis has come mainly from stock-recruitment analysis (fitted stock-recruit curves differ between cycle years; J. Woodey, IPSFC, pers. comm.), from the ability of the hypothesis to explain variations in cycle patterns among stocks and over time, and from field studies indicating that predators do indeed consume many juveniles (see review in Steigenburger and Larkin 1974; also IPSFC 1976). However, juvenile abundance estimates for Shuswap Lake (Adams Stock) do not support the hypothesis that survival of underyearling fry is cyclic (Vernon 1982), and the stock-recruitment analyses could be biased due to errors in variables and time series effects (Walters 1985a). Other mechanisms have been proposed to explain cyclic dominance (changes in plankton food supplies, high fishing rates on low runs, etc). But for each of these mechanisms, as for the Ward–Larkin predation hypothesis, field studies have led to ambiguous or contradictory evidence.

It appears worthwhile now to ask whether cyclic dominance is a real phenomenon (in the sense of depensation and interaction between cycle years), or might instead be due simply to historical accidents that have established differences in abundance (between the cycle years) which are now maintained by exploitation patterns. If the phenomenon is real, there should exist clear differences in stock-recruitment parameters between cycle years, no matter where in the life cycle the depensatory effects actually occur, and there should be cyclic patterns in the residuals from aggregate stock-recruit curves fitted to pooled data from all cycle years. This paper examines stock and recruitment statistics for Fraser River stocks over the period 1948–84. Recruitment and escapement estimates for these stocks have been developed by staff of the International Pacific Salmon Fisheries Commission (IPSFC) using various procedures for estimating stock contributions to mixed fishery catches (J. Woodey, IPSFC, pers. comm.). Here we present only summary calculations that are subject to revision when the IPSFC staff have completed their stock reconstructions and analyses; we are grateful to the staff for consultation and advice about interpretation of the data.

TABLE 1. Corrected and uncorrected estimates of Ricker stock-recruitment parameters for eight Fraser River sockeye stocks. Dominant cycles indicated by * in the left column.

Stock name	Ricker productivity	Corrected productivity	Equilibrium stock size eff. females	Corrected stock size eff. females
Birkenhead				
All Years	2.90	2.90	203 635	270 774
Cycle 1980	2.72	2.65	176 552	189 926
Cycle 1981	3.07	2.93	116 843	198 305
Cycle 1982	2.81	2.63	368 222	309 736
Cycle 1983	3.22	3.15	138 426	129 774
Chilko				
All Years	2.59	2.56	1 061 177	1 947 552
Cycle 1980	2.99	2.96	795 773	807 680
Cycle 1981	2.47	2.28	199 924	139 223
Cycle 1982	3.58	3.56	220 691	224 651
Cycle 1983*	2.95	2.91	875 067	817 712
Late Shuswap				
All Years	2.33	2.24	3 611 065	15 947 490
Cycle 1980	2.46	2.37	11 625	11 417
Cycle 1981	4.07	4.21	4 739	4 448
Cycle 1982*	3.24	3.18	2 089 256	1 711 479
Cycle 1983	2.52	2.15	1 322 979	1 067 165
Weaver				
All Years	2.56	2.49	162 883	203 673
Cycle 1980	2.34	2.11	103 377	9 329
Cycle 1981	2.67	2.50	154 324	133 315

TABLE 1. (Continued.)

Stock name	Ricker productivity	Corrected productivity	Equilibrium stock size eff. females	Corrected stock size eff. females
Cycle 1982	2.49	2.16	488 547	405 557
Cycle 1983	3.15	3.15	50 299	47 413
Stellako				
All Years	2.62	2.65	410 105	739 039
Cycle 1980	2.97	2.87	112 785	85 763
Cycle 1981	2.94	2.83	81 988	90 287
Cycle 1982	2.26	1.58	−1 542 752	−999 139
Cycle 1983*	3.34	2.34	268 126	234 247
Horsefly				
All Years	2.82	2.74	4 333 616	15 369 320
Cycle 1980	3.88	3.94	370	357
Cycle 1981	3.02	2.90	1 226 398	1 158 557
Cycle 1982	2.70	2.36	662 614	578 391
Cycle 1983	3.15	3.20	2 122	2 161
Early Stuart				
All Years	2.46	2.48	520 041	1 042 416
Cycle 1980	2.86	2.73	46 173	66 638
Cycle 1981*	3.24	3.09	333 713	480 448
Cycle 1982	2.64	2.54	68 224	158 945
Cycle 1983	3.22	3.11	86 164	158 832
Late Stuart				
All Years	2.74	2.62	571 595	463 527
Cycle 1980	4.15	4.15	3 694	3 636
Cycle 1981*	3.42	3.33	422 209	397 442
Cycle 1982	3.74	3.67	18 231	18 892
Cycle 1983	3.53	3.41	14 569	13 752

Stock-Recruitment Assessment Procedures

For each of the eight stocks listed in Table 1, IPSFC staff have compiled estimates of total escapement, effective female escapement (females weighted by size-age compositions to give a total abundance standardized to 4-yr-old female equivalents), and recruits from each brood year 1948–79 by freshwater and total age of the returning recruits. Here we will examine mainly the total adult returns (age 4–6, predominantly age 4) R_t for each brood year t, in relation to the effective female escapement E_t. This choice can have a large effect as compared to using total escapements, especially for very small (off cycle) runs on the cycle year just prior to each dominant run; in such years, the total escapement can consist mostly of age 3 "jack" males produced by the previous dominant run. Including those males in assessments of productivity per spawner would obviously make the low cycle years look less productive, hence giving a misleading appearance of depensatory effects at low stock sizes.

Following the procedure suggested by Walters (1985a), we first carried out standard stock-recruitment regressions of log (R_t/E_t) versus E_t, to provide initial estimates a and b in the stochastic Ricker model log $(R_t/E_t) = a - bE_t + w_t$ where the w_t are "random" effects on the productivity index log (R_t/E_t) due to factors other than the compensatory effects of increasing escapement (as measured by bE_t). Then using the initial (1948–51) escapements, estimated historical exploitation rates (1951–84), and estimated variance of w_t for each data set (stock-cycle year combination), we did 100 Monte Carlo simulations (with $a = \hat{a}$, $b = \hat{b}$, *and normally distributed* w_t values) of the E_t - R_t time series and applied standard regression analysis to the results of each simulation. The averaged estimates a_1 and b_1 from the simulations allowed us to calculate initial estimates of the biases a_1 - a and b_1 - b expected from using standard regressions in a time series setting where the R_t and E_t are not independent random variables. Then for each data set we repeated the 100 simulations using 0.7 â and 0.7 b̂ as the "true" parameter values, to get a second set of averaged parameter estimates a_2 and b_2 and a second set of bias estimates. Then assuming that the bias is linearly dependent on a and b (i.e., $\hat{a} = r + sa$) we obtained bias corrected estimates as:

$$\bar{a} = \frac{0.3\hat{a}^2 - 0.3\hat{a}a_1 + \hat{a}(a_2 - a_1)}{(a_2 - a_1)} \qquad (1)$$

$$\bar{b} = \frac{0.3\hat{b}^2 - 3\hat{b}b_1 + \hat{b}(b_2 - b_1)}{(b_2 - b_1)}$$

In general, these estimates are expected to be lower than the biased estimates $\hat{a}$ and $\hat{b}$ (Walters 1985a), implying that the stocks are less productive at low escapement levels (smaller

a values) and have higher unfished equilibrium levels (smaller b values) than indicated by $\hat{a}$ and $\hat{b}$.

For each stock we also calculated regression estimates $\bar{a}_p$ and $\bar{b}_p$ for data pooled across the cycle years, and did Monte Carlo simulations using these pooled estimates as the "true" a and b values rather than the $\bar{a}$ and $\bar{b}$ estimates from the individual cycle year time series (but still starting from the observed 1948–52 escapements and using the observed exploitation time series for each cycle year). These calculations should demonstrate whether the bias in a and b estimates depends on how low the initial stock size is compared to the unfished equilibrium. Preliminary Monte Carlo simulations for fake populations subject to constant, high exploitation rates had indicated that the fitted stock-recruitment curve will tend to bend over at a small multiple of the average stock size, i.e., be grossly biased toward predicting that low stocks should not recover much following a reduction in exploitation rates.

The correction procedures described above may not remove all biases that would falsely lead to apparent differences in stock-recruitment relations among cycle years. As a further test for such differences, we examined the autocorrelation patterns of residuals from the pooled (all cycle years) regressions. If depensatory effects are present, these residuals should have a cyclic pattern reflected by significant autocorrelations at lags of 1–4 years. For each time lag k, the autocorrelation r_k was estimated as (Box and Jenkins 1976)

$$(2) \qquad r_k = \sum_{t=1}^{N-k} \bar{w}_t \bar{w}_{t+k} \Big/ \sum_{t=1}^{N} \bar{w}_t^2$$

where $\bar{w}_t = \log (R_t/E_t) - \bar{a}_p - \bar{b}_p E_t$ and $N = 32$ data points for each pooled series.

All eight of the stocks may have been subject to common environmental effects during freshwater or ocean rearing for at least some brood years, and such effects may not have been randomly distributed over time. We attempted to estimate these effects by a procedure detailed in Walters (1986), in which the Ricker model is written in an extended (general linear model) form as $\log (R_{it}/E_{it}) = a_i - b_i E_{it} + w_{it} + w_t{}^*$ where the index i refers to stock, the w_{it} are stock-specific environmental effects and $w_t{}^*$ is a (density-independent) common effect measured relative to the stock specific a_i values (so the $w_t{}^*$ can follow any time pattern but $\Sigma\, w_t{}^* = 0$). By separating out the common effects $w_t{}^*$, we hoped to see less noisy stock-recruitment relations and possibly a cyclic time pattern in the $w_t{}^*$ that might be partly responsible for the development of cyclic dominance.

It is conceivable that interactions among cycle years could produce patterns of variation in productivity (recruits/spawner) that are not evident as autocorrelated or cyclic residuals from the overall recruitment relationship. However, if a particular cycle year is influenced by others, then its productivity should show some statistically detectable variation or regression effect in relation to departures of the other cycle years from their average historical abundances. We attempted to detect such variation by fitting the data to another extended Ricker model, of the linear regression form

$$(3) \qquad \log (R_{it}/E_{it}) = a_i - b_i E_{it} + \sum_{k=1}^{3} b_{ik} E_{i,\, t-k} + w_{it}$$

Here R = recruits, E = eggs, and the a_i and b_i represent productivity and density dependence within the i^{th} *stock*. The b_{ik} represent effects of varying abundances of other cycle years, assuming that effective female escapements $E_{i,\, t-k}$ in those cycle years are reflective of impacts that may occur on the juveniles produced by E_{it}. There is cause for management concern if any b_{ik} is significant and negative; in that event, increases in the cycle t-k escapements $E_{i,\, t-k}$ would lead to decreased productivity in the t^{th} *cycle line.*

Results

The standard linear regressions of log (R/E) vs E would suggest that there are substantial differences among stocks and in some cases, among cycle years within stocks (Table 1). For the stocks that show strong cyclic variation in escapement, the Ricker $\hat{a}$ values are generally higher for the weakest offcycle (lowest abundance) brood year, as are the Ricker $\hat{b}$ values; if the estimates were not biased, this pattern would indicate that the offcycle spawning stocks have higher productivity per female but much lower equilibrium stock sizes (i.e., more steeply dome shaped recruitment curves) than the dominant and subdominant cycle years. These results are in immediate conflict with the Ward–Larkin predation hypothesis, which predicts lower productivity per female in the offcycle years, but are in agreement with the juvenile abundance data for Shuswap Lake mentioned above. Only the Chilko stock showed consistently lower productivity for the lowest offcycle year (1981), which would be indicative of depensatory predation effects.

As expected, the $\bar{a}$ and $\bar{b}$ estimates (partially corrected for bias due to time series correlations) were generally lower (Table 1), indicating lower productivity and higher equilibrium stock sizes. The corrected estimates still support the hypothesis that there are differences in recruitment curves among cycle years for stocks that have shown strong cyclic variation in escapement. However, these estimates remain suspect, since the corrections were developed by examining biases expected for true $\bar{a}$ and $\bar{b}$ values in the neighborhood of the uncorrected estimates $\hat{a}$ and $\hat{b}$. It is particularly suspicious that the estimated recruitment curves generally bend over at escapement levels that are small multiples of the historical average escapements. Figure 1 shows that this effect is likely due to bias in the regression estimation procedure, rather than real differences between cycles. We set up a simulated stock with a and b parameters and environmental variability similar to the Adams River dominant cycle year, then fished this stock down to low levels (average escapements E = 0.03, 0.15, 0.3 million effective females) by using high and constant exploitation rates. We then took 100 samples of 10 successive cycles at each escapement ($\bar{E}$) level, and calculated averages of the standard regression estimates a and $\bar{b}$ across the 100 runs; the curves plotted in Fig. 1 represent these averages. Had the regression estimates been unbiased, the curves for the three $\bar{E}$ levels should have closely matched the true model curve, since we did not put any difference into the a and b values between cycle years for the simulated population.

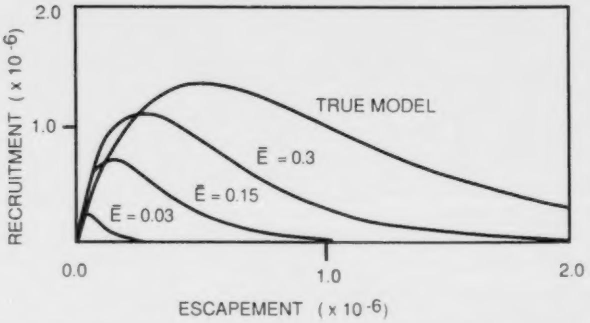

FIG. 1. Expected stock recruitment relations estimated given 10 cycles of data for a hypothetical sockeye population that follows the recruitment relation marked "TRUE MODEL" for all cycle years. For each biased estimate, the stock was subject to a constant exploitation that would hold it (on average) near the average escapements E as noted. The point of this figure is that the recruitment function estimated by standard regression methods will tend to bend over in the neighborhood of the historical average escapement level, even if the stock could in fact be greatly increased.

Considering the magnitude of possible bias indicated by Fig. 1, we attempted to construct a simple test of the null hypothesis that all cycle years for each stock have the same recruitment relationship, namely that relationship which best fits the data aggregated across cycle years. For each cycle year, we generated 1000 Monte Carlo simulations of the cycle year's performance to 1984, starting each simulation with the observed 1948–52 initial escapement and applying the observed exploitation rates over time, while calculating recruitments from the aggregate stock-recruitment relationship ($\bar{a}_p$ and $\bar{b}_p$) with random errors w_t. Ricker a and b parameters were estimated for each simulation, and the distribution of these estimates was used to define approximate 95% confidence limits for the null hypothesis (as the ranges within which 95% of the 1000 a and b estimates fell). These limits (Tables 2a and 2b) did not encompass the uncorrected estimates for only a few stock-cycle year cases, indicating that in general it is not possible to reject the null hypothesis of a common recruitment relationship for all cycle years. The departures that were significant all involved Ricker a values higher than predicted by the null hypothesis, for cycle years just prior to the dominant or subdominant year. Recruitment estimates for these low cycles are obtained as a mix mainly of 4_2 and 5_3 fish, where the 5_3 contribution represents a very small sampled proportion of the fish in the dominant run; it is therefore possible that "minor" ageing or sampling errors (4_2 dominant cycle fish being classified as 5_3 returns from subdominant spawning) have caused the offcycle recruitments to be overestimated.

Further evidence that variation between cycle years is not patterned as predicted by cyclic dominance hypotheses is provided in Table 3, which presents autocorrelations at lags 1–8 in deviations from overall Ricker curves fitted to the 32 brood years data for each stock. There is not one significant correlation in the entire table, indicating that the residuals w_t can be adequately modelled as independent environmental effects (no coupling among cycle years).

No striking pattern was obtained when we estimated the common environmental effects w_t^* that are apparently shared among stocks (Fig. 2). None of those estimated effects is significantly different ($P < 0.05$) from 0, and they are all small compared to the stock-specific residuals w_{it}. They do not appear to follow a temporal pattern suggestive of some long term "cycle" in environmental conditions, in contrast to the findings of Wong (1982; see also Walters 1985b) from analyses of aggregate stock-recruitment data for the total Fraser River sockeye population.

Table 4 presents estimates of the cross-cycle-year regression coefficients b_{ik} of eq. (3). Most of these coefficients are of the magnitude and sign (-) that indicate a risk of depressing some cycle years by trying to increase abundance in others. However, only a few of the coefficients are significantly different from zero. There are no strong positive coefficients that may indicate "smolt buffering" as propos-

TABLE 2a. Ricker a estimates compared to bounds estimated by simulation given no cyclic dominance. ** indicates significant departures

Stock name	Ricker productivity uncorrected	Lower bound productivity	Median productivity	Upper bound productivity
Birkenhead				
All Years	2.90	2.58	2.90	3.34
Cycle 1980	2.72	2.21	3.01	3.80
Cycle 1981	3.07	1.97	3.00	4.00
Cycle 1982	2.81	2.08	2.91	3.69
Cycle 1983	3.22	2.24	2.90	3.56
Chilko				
All Years	2.59	2.32	2.56	2.94
Cycle 1980	2.99	1.91	2.73	3.69
Cycle 1981	2.47	2.09	2.71	3.34
Cycle 1982	**3.58	2.05	2.64	3.17
Cycle 1983	2.95	1.99	2.65	3.30
Late Shuswap				
All Years	2.33	1.97	2.24	2.67
Cycle 1980	2.46	1.60	2.52	3.41
Cycle 1981	**4.07	1.66	2.52	3.42

TABLE 2a. (*Continued.*)

	Ricker productivity uncorrected	Lower bound productivity	Median productivity	Upper bound productivity
Cycle 1982	3.24	1.65	2.59	3.61
Cycle 1983	2.52	1.80	2.50	3.44
Weaver				
All Years	2.56	2.06	2.49	3.08
Cycle 1980	2.34	1.54	2.69	3.72
Cycle 1981	2.67	1.62	2.63	3.61
Cycle 1982	2.49	1.50	2.62	3.64
Cycle 1983	3.15	1.78	2.65	3.77
Stellako				
All Years	2.62	2.37	2.65	2.92
Cycle 1980	2.97	2.06	2.73	3.29
Cycle 1981	2.94	2.18	2.78	3.76
Cycle 1982	2.26	2.07	2.75	3.64
Cycle 1983	3.34	2.14	2.79	3.64
Horsefly				
All Years	2.82	2.49	2.74	3.07
Cycle 1980	**3.88	2.21	2.87	3.52
Cycle 1981	3.02	2.35	3.13	3.94
Cycle 1982	2.70	2.10	2.86	3.66
Cycle 1983	3.15	2.03	2.74	3.52
Early Stuart				
All Years	2.46	2.14	2.48	2.81
Cycle 1980	2.86	1.88	2.57	3.32
Cycle 1981	3.24	1.77	2.64	3.60
Cycle 1982	2.64	2.04	2.63	3.45
Cycle 1983	3.22	2.04	2.71	3.73
Late Stuart				
All Years	2.74	2.24	2.62	3.22
Cycle 1980	**4.15	1.72	2.69	3.66
Cycle 1981	3.42	1.93	2.83	4.16
Cycle 1982	3.74	1.83	2.81	3.88
Cycle 1983	3.53	1.80	2.90	3.94

TABLE 2b. Uncorrected equilibrium stock size estimates compared to bounds estimated by simulation. ** indicates significant departures.

Stock name	Equilibrium stock size eff. females	Lower bound stock size eff. females	Median stock size eff. females	Upper bound stock size eff. females
Birkenhead				
All Years	203 635	145 494	186 145	250 025
Cycle 1980	176 552	87 973	155 831	596 909
Cycle 1981	116 843	−323 910	122 375	328 352
Cycle 1982	368 222	123 240	181 807	380 932
Cycle 1983	138 426	114 792	177 810	450 891
Chilko				
All Years	1 061 177	635 808	924 189	1 383 797
Cycle 1980	795 773	461 581	898 659	2 009 566
Cycle 1981	199 924	282 832	744 596	2 719 919
Cycle 1982	220 691	193 832	776 296	2 440 480
Cycle 1983	875 067	−2 182 583	340 029	4 264 093

TABLE 2b. (*Continued.*)

	Equilibrium stock size eff. females	Lower bound stock size eff. females	Median stock size eff. females	Upper bound stock size eff. females
Late Shuswap				
All Years	3 611 065	837 105	2 948 033	6 611 114
Cycle 1980	11 625	−3 373 593	−149 936	4 506 459
Cycle 1981	4 739	−8 443 834	23 229	4 256 761
Cycle 1982	2 089 256	462 931	2 486 297	5 434 632
Cycle 1983	1 322 979	−23 910	2 217 658	5 692 089
Weaver				
All Years	162 883	102 542	145 774	199 092
Cycle 1980	103 377	7 795	108 597	335 401
Cycle 1981	154 324	30 178	131 111	296 642
Cycle 1982	**488 546	33 929	137 359	276 173
Cycle 1983	50 299	21 276	127 297	240 891
Stellako				
All Years	410 105	232 950	357 356	487 056
Cycle 1980	112 785	19 180	248 773	1 098 263
Cycle 1981	81 988	85 991	260 676	714 857
Cycle 1982	**−1 542 752	160 732	320 027	680 170
Cycle 1983	268 126	70 242	283 700	1 088 274
Horsefly				
All Years	4 333 616	−16 923 690	148 386	12 199 260
Cycle 1980	370	−701 538	−128 136	1 209 802
Cycle 1981	1 226 398	−1 901 072	530 779	8 761 658
Cycle 1982	662 614	−8 836 745	−319 743	17 246 570
Cycle 1983	2 122	−2 275 468	+190 728	1 199 098
Early Stuart				
All Years	520 041	230 774	443 895	657 015
Cycle 1980	46 173	−437 981	158 961	3 939 591
Cycle 1981	333 713	178 721	393 874	1 071 608
Cycle 1982	68 224	30 103	315 024	941 850
Cycle 1983	86 164	49 056	262 147	783 035
Late Stuart				
All Years	571 595	94 678	463 527	1 078 274
Cycle 1980	3 694	−1 407 364	55 729	1 749 837
Cycle 1981	422 209	14 591	365 659	955 453
Cycle 1982	18 231	−304 867	308 922	1 383 051
Cycle 1983	14 569	−429 015	98 233	1 214 756

TABLE 3. Lagged correlations of deviations from aggregated stock recruitment relationships (all years).

Time lag (yr)	Birkenhead	Chilko	Late Shuswap	Weaver	Stellako	Horsefly	Early Stuart	Late Stuart
1	0.207	0.177	0.278	0.260	−0.228	−0.173	0.220	0.208
2	0.140	−0.259	−0.053	0.316	−0.292	0.024	0.255	0.198
3	0.159	−0.169	−0.220	0.250	0.159	0.012	−0.003	0.270
4	0.155	0.244	−0.108	0.048	−0.053	−0.340	0.211	0.162
5	0.054	0.020	−0.259	0.157	−0.029	−0.056	−0.035	0.014
6	−0.126	−0.247	−0.309	0.078	−0.047	0.021	−0.018	−0.026
7	0.009	−0.317	−0.120	−0.004	−0.057	0.047	−0.212	−0.136
8	0.130	0.117	0.205	0.090	0.220	0.239	0.034	−0.226

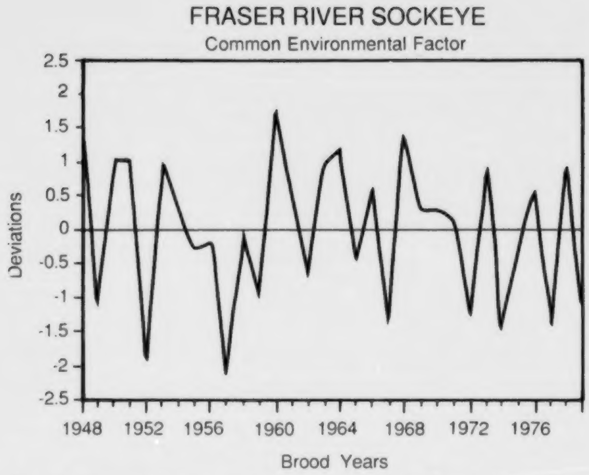

FIG. 2. Temporal pattern of common residuals from stock recruitment curves of eight Fraser River stocks. The deviation plotted for each year is the estimated value of w^* in the extended recruitment model $\log(R/E) = a - bE + w_{\text{stock}} + w^*_{\text{common}}$; the w^* are "random" (density independent) effects on productivity that apparently have affected all stocks simultaneously.

ed by Ward and Larkin (1964). The statistical significance of the estimates must be interpreted with caution, since most stocks have showed such consistent cycle patterns that there is little informative contrast among the E_{it} and $E_{i,\,t-k}$ values. Note that half of the regression coefficients for effects within brood years (b_i) are also not significant, suggesting that such stocks are so depressed that no clear density dependence is evident, let alone cross-cycle interactions.

Discussion

The Fraser River stock and recruitment data generally do not support the hypothesis that cyclic dominance is due to inherent differences in productivity among cycle years. Apparent differences among recruitment curves for stocks like the Adams and Horsefly are very likely due to biases in the estimation of these curves. The precise explanation for these biases involves a somewhat complicated statistical argument (Walters 1985a); intuitively, the basic problem is that a nonrepresentative sample of stock-recruit data points is obtained whenever a stock is harvested for only a short period of time (8–10 cycles is short in a statistical sense) with relatively steady exploitation rates. Above average survivals at the lowest stock sizes are overrepresented in the sample, since these good survivals tend to push the stock up away from the lowest levels; the net result is to overestimate the Ricker a parameter. Likewise, below average survivals are overrepresented for the larger stock sizes since these survivals tend to push the stock back down; the net result is to overestimate the Ricker b parameter (underestimate equilibrium stock size). Thus the problem is not just with the particular recruitment equation or statistical formula for estimation; there is a more fundamental problem that the few data points for each cycle year are likely to be a misleading sample in relation to average, long-term potential productivity. As yet, no fully satisfactory statistical method has been devised to correct for this problem.

Though there do not appear to be significant inherent differences among cycle years, there may well be interactions among the cycles as evidenced by the signs of the regression coefficients in Table 4. Though at least some of the coefficients are probably statistical artifacts arising from high correlation in escapements among cycle years, there are enough significant values to indicate that management directed at rehabilitation of offcycles should proceed with caution and regular reevaluation of productivity data (so as to determine whether the oncycle runs are indeed being depressed).

If there are no major differences in productivity among cycle years, beyond effects expected from sex/age ratios of spawners, then why have the observed dominance patterns persisted? A first answer is that the patterns have not been all that persistent; there have been substantial increases in some offcycle runs, and on at least one occasion a growing stock (the Adams River subdominant cycle year) was deliberately fished down (90% exploitation in 1971) to avoid having the fishery for it interfere in later years with efforts to rehabilitate pink salmon runs (IPSFC 1972). A second answer is that exploitation rates have generally been very high, and even a few years of "low" (40–60%) exploitation rates (as occurred on the lowest Adams offcycle during the 1960s) would not be sufficient for the lowest offcycle runs to recover to significant sizes relative to the dominant

TABLE 4. Regression coefficients for effects of past escapements on productivity [log (recruits/effective female spawner)] of eight major sockeye stocks. Regression model defined by equation (3). Statistical significance indicated by *: $P < 0.05$ and **: $P < 0.01$ for t-tests on the individual coefficients.

	Coefficients (× 10⁶)			
Stock (i)	Escapement in brood year (b_i)	Escapement one year earlier (b_{i1})	Escapement two years earlier (b_{i2})	Escapement three years earlier (b_{i3})
Birkenhead	7.23	−9.38	0.85	11.23
Chilko	2.90*	−4.20**	−1.22	0.17
Adams	1.82**	−1.17	−1.72*	−0.53
Weaver	23.5	26.4	−15.3	−0.43
Stellako	7.12	−2.48	−5.29	−7.14
Horsefly	7.32	−8.38	−5.34	−12.44
Early Stuart	8.58*	−10.32**	−2.56	−5.42
Late Stuart	10.42*	−9.46*	−8.85*	−7.21

runs. For example, a stock of 1000 females, with a Ricker a value of 2.4 (see Table 1) and a 50:50 sex ratio, would require 10 cycles to reach a level of 50 000 females if the exploitation rate were 70% on each cycle; this level would still look small compared to a dominant run of (say) 1 000 000 females. A third answer is that low runs may indeed be somewhat less productive due to depensatory predation effects, but these effects may be masked by errors in estimates of recruitment (i.e., in small contributions to large mixed-stock catches); high exploitation rates combined with slightly lower productivity could certainly account for the observed behavior of even the most depressed runs.

As in the Bristol Bay sockeye study reported by Eggers and Rogers (1987), the Fraser stocks that show strong cyclic variation (Chilko, Late Shuswap or Adams, Horsefly, Late Stuart) have also apparently been subject to higher exploitation rates in the offcycle years. If the IPSFC's abundance estimates for the lowest offcycle years are reliable, then these runs have typically been exploited at rates of around 80%, while the cycle years have usually enjoyed rates below 70%.

Though accidental reductions in run size followed by continued high (and perhaps depensatory) fishing rates can explain recent patterns of variation in abundance between cycle years, such explanations cannot account for the persistent dominance patterns documented from over a century of historical records by Ward and Larkin (1964). Since the stock-recruitment data for 1948-84 do not support the assumption of strong variation in productivity among cycle years, it would be worthwhile to take a harder look at the assumption that exploitation rates were low on all cycle years prior to the late 1800's. The Native Indian fishery was a substantial and complex gauntlet along the Fraser River (Hewes 1973), and may well have exerted strong depensatory effects on smaller runs of the various stocks. Even the current Indian catch rates of around 300 000—500 000 sockeye per year (Schubert 1982) appear to be nearly independent of stock size (i.e., depensatory) and represent an exploitation rate of at least 20-30% on offcycle escapements past the commercial fishing areas.

Over the long run, it appears that there are major opportunities to increase yields by encouraging recovery of various offcycle runs. Some of these opportunities are currently being pursued, with very encouraging results. Others involve some very difficult tradeoffs, especially for the mid-timing complex of stocks that are harvested together during late July and early August. These tradeoffs involve giving up catch from dominant runs of some stocks in order to rebuild offcycle runs of other stocks (Table 5). Some slow stock rebuilding would be accomplished by a general lowering of exploitation rates to the 50-60% levels that the corrected stock-recruitment estimates indicate are optimal. Such a policy would eventually result in average annual yields 10-20% higher than historical average even if the lowest offcycle runs for the Adams and Horsefly stocks never recover; we estimate that the present net economic value of these increases, using current sockeye landed values and a 3% real discount rate, would be in the order of $150 million-$300 million (Fig. 3). An alternative extreme would be to impose a complete moratorium on fishing in some timing/cycle year windows. Between these extremes there should exist a wise compromise policy that involves giving up some catches in the short term in favor of substantially larger and more stable harvests in the long run. A major challenge now is to identify that compromise.

TABLE 5. Principal conflicts in rehabilitation of mid-timing sockeye stocks. For each cycle year (1904 = 1980, 1907 = 1983) catches from the strong stocks as noted would have to be foregone in order to rebuild the weak stocks as noted.

Cycle year	Strong stocks	Weak stocks
1904	Chilko	Horsefly, Seymour, Early and Late Stuart, Stellako
1905	Horsefly, Early and Late Stuart	Chilko, Stellako
1906	—	Chilko, Horsefly, Stellako, Late Stuart
1907	Chilko, Stellako	Horsefly, Stellako, Late Stuart

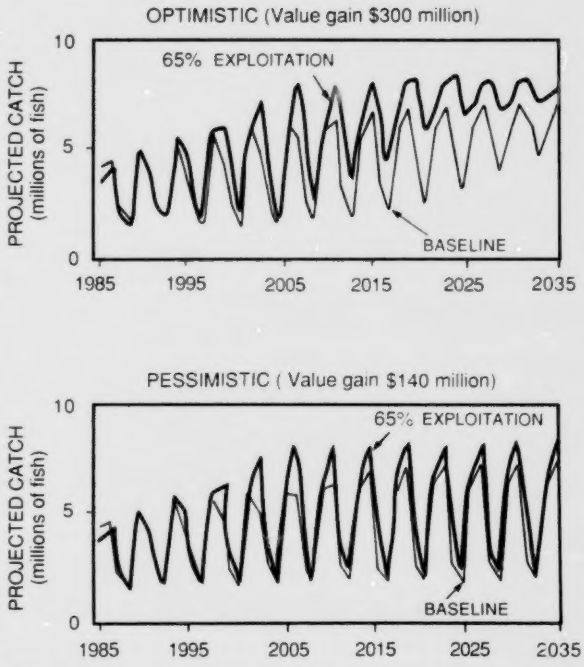

FIG. 3. Fifty-year simulations of aggregate catch from the eight major sockeye stocks of the Fraser River, initialized with 1980-83 escapements and calculated from Ricker stock recruitment models with the "all years" uncorrected parameter estimates in Table 1. For both panels, the baseline prediction was obtained by applying a 75% exploitation rate to all stocks in all years, while the rehabilitation prediction was obtained by applying a 65% exploitation rate to all stocks in all years. In the bottom (pessimistic) panel, we arbitrarily kept all very low (< 10 000 spawner) offcycle stocks from increasing by holding their escapements at 1980-83 levels. Economic value for each panel was calculated by adding up the discounted (3%/yr.) catch differences between the two predictions, times a conservative net landed value of $10 per fish.

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Managing the Skeena River Sockeye Salmon (*Oncorhynchus nerka*) Fishery — the Process and the Problems

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Abstract

SPROUT P. E., AND R. K. KADOWAKI 1987. Managing the Skeena River sockeye salmon (*Oncorhynchus nerka*) fishery — the process and the problems, p. 385–395. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Managing the Skeena River sockeye fishery in north coastal British Columbia is an intricate task complicated by biological uncertainties and multiple objectives. This paper traces the development of management of the Skeena fishery from its modest start at the beginning of this century to the present complicated hierarchical decision-making structure. The major components of the present management process are: (1) developing concurrent biological, economic, social, and legal objectives, (2) forecasting run size and formulating fishing plans, (3) consulting with user groups, (4) finalizing fishing plans, (5) executing fishing plans, and (6) evaluating management impact on the resource. The Skeena sockeye run is composed of over 50 stocks, with two enhanced stocks producing most of the run. Timing overlaps in the harvest area between enhanced and unenhanced sockeye and runs of pink, chum, coho, chinook, and steelhead trout have created problems in optimally managing each species. Explicit statement of objectives and specifying decision making procedures may improve management.

Résumé

SPROUT, P. E., AND R. K. KADOWAKI. 1987. Managing the Skeena River sockeye salmon (*Oncorhynchus nerka*) fishery — the process and the problems, p. 385–395. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

La gestion de la pêche du saumon nerka dans la rivière Skeena sur la côte nord de la Colombie-Britannique est une tâche complexe qui est compliquée par des incertitudes biologiques et des objectifs multiples. Le présent article retrace le développement de la gestion de la pêche dans la rivière Skeena depuis son début modeste au début du siècle jusqu'à la structure actuelle hiérarchique compliquée de prise de décision. Les éléments importants du processus actuel de gestion sont : 1) l'établissement d'objectifs concordants sur les plans biologique, économique, social et juridique, 2) la prévision de l'importance de la remonte et l'élaboration de plans de pêche, 3) la consultation de groupes d'utilisateurs, 4) l'établissement définitif des plans de pêche, 5) la réalisation des plans de pêche, et 6) l'évaluation des répercussions de la gestion sur la ressource. La remonte de saumon nerka dans la Skeena est constituée de plus de 50 stocks, deux stocks mis en valeur étant responsables de la plus grande partie de la remonte. Les chevauchements des moments de remonte dans le secteur d'exploitation des saumons nerkas mis en valeur et de ceux qui ne l'ont pas été de même que les remontes de saumon rose, kéta, coho, quinnat et de la truite arc-en-ciel ont créé des problèmes pour la gestion optimale de chaque espèce. On peut améliorer la gestion en faisant un énoncé explicite des objectifs et en précisant les mécanismes de prise de décisions.

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Introduction

The management of modern salmon fisheries is complicated by high user demand, mixed stocks of different productivities, and conflicting biological, social, and economic policies. Management objectives may not be explicit and are seldom priorized, yet it is the responsibility of the fisheries manager to make biologically sound and socio-economically responsible harvesting decisions. Hilborn and Walters (1977), Keeney (1977), and Healey (1984) have proposed quantitative techniques for developing management objectives but so far there is little evidence that their techniques are being applied in the British Columbia salmon fisheries. In an environment of high uncertainty, competitive economic and social interests, and delicate biological balances, resource management objectives must be explicit and understood clearly by both the management agency and the user groups and they must permit measurement of management performance (ACMRR 1980; Wilimovsky 1985).

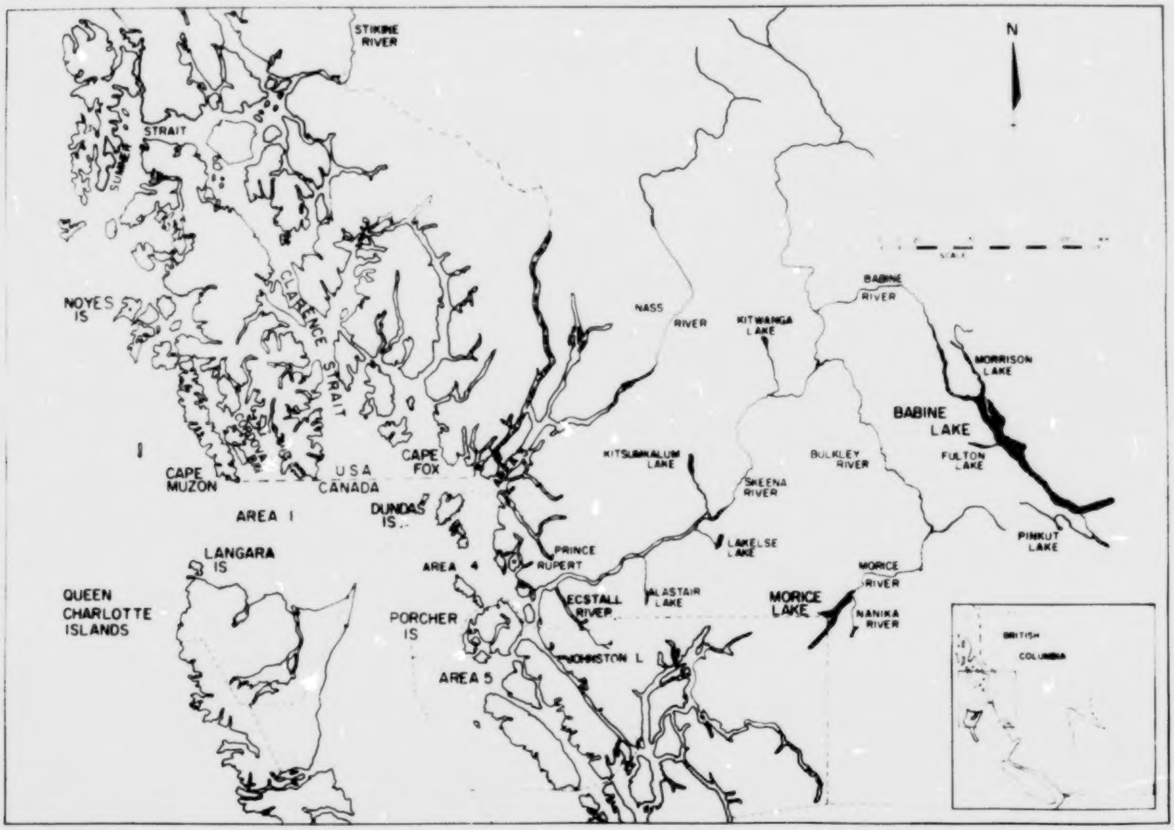
The Skeena River drains into the Pacific Ocean just south of the B.C.-Alaska border (Fig. 1). It is second only to the Fraser in British Columbia in terms of the number of salmon it produces.

The Skeena River sockeye fishery is a classic example of a complex resource management system. Seine, gillnet, and troll fishermen, Indian food fishermen, and sport fishermen share the Skeena salmon harvest. Each group has its own economic and social objectives and all come under varying degrees of control by the fisheries management agency, the federal Department of Fisheries and Oceans (DFO). These fisheries will be described later in this paper.

Overlaps in run timing prevent harvesting of single stocks while diverse stock productivities preclude applying a single harvest rate to provide the maximum sustained yield for all stocks (Larkin and McDonald 1968; Takagi and Smith 1973; DFO 1985).

In the face of these complexities in managing Skeena River sockeye, a hierarchical decision-making structure has evolved that attempts to synthesize the variety of biological, economic, and social inputs in order to make the best decision under the circumstances.

The purposes of this report are: (1) to review the development of the management of Skeena sockeye, (2) to describe the current process of managing the Skeena sockeye fishery with emphasis on objective setting and in-season decision making, and (3) to recommend improvements to the management system.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QUEEN CHARLOTTE ISLANDS
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PORCHER IS
AREA 5
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ALASTAIR LAKE
NASS RIVER
KITWANGA LAKE
KITSUMKALUM LAKE
SKEENA RIVER
LAKELSE LAKE
BULKLEY RIVER
BABINE RIVER
MORRISON LAKE
BABINE LAKE
FULTON LAKE
PINKUT LAKE
MORICE RIVER
MORICE LAKE
NANIKA RIVER
SCALE
BRITISH COLUMBIA

FIG. 1. North coastal British Columbia and southeast Alaska showing the Skeena River and major fishing areas for Skeena sockeye (see text for names of fishing locations).

Evolution of the Management Process

The evolution of the management process can conveniently be divided into three major periods which are characterized by different approaches to the science and politics of fisheries resources management. We will refer to these as the pre-research, research, and current periods. In the pre-research period (1876–1942) the motivation and ability to harvest Skeena sockeye far exceeded the biological understanding. Although slow progress was made in biological investigation during this period, it was not until the research period (1943–71) that a coordinated scientific program was implemented. In the current period (1972-present) the socio-economic and political aspects of resource management have gained in prominence and are the subject of much work by fisheries managers and biologists. Each period is discussed in some detail in the following sections.

PRE-RESEARCH PERIOD (1876 TO 1942)

The first Skeena River salmon cannery began operation in 1876. It was not until 1889, however, that general fishery regulations were approved for the Province of B.C. Until then the canneries, which had increased to five, controlled the opening and closing of fishing and specified the type of gear needed to meet their production requirements. Commissions were appointed in 1890 and 1891 by the federal government to investigate the B.C. salmon fisheries and make recommendations for a more comprehensive set of regulations. New regulations were issued in 1894, and seasonal restrictions for all salmon species and a weekly closed period were established (Carrothers 1941). Gear restrictions, licensing procedures, Indian food fishery, and industry canning guidelines were also covered. Apart from the enforcement of these regulations, early involvement by the federal government amounted to facilitating the commercial exploitation of the resource; for example, the removal of sunken logs which could damage gillnets was one of the high priority tasks recommended by early fishery managers and for this purpose a specially equipped barge was brought to the Skeena in 1907 (Department of Marine and Fisheries 1907).

By the turn of the century it became apparent that without an annual appraisal of sockeye escapement on the spawning grounds, it would be impossible to determine if the commercial fishery was over- or underexploiting the run. The first exploratory trip to Babine Lake, the major sockeye producer in the Skeena drainage, was made by fishery "overseers" in 1904 (Department of Marine and Fisheries 1905) and over the next few years much of the rest of the watershed was extensively explored. These pioneers focused on the qualitative estimation of escapement and removal of natural and man-made obstructions to spawning.

In 1910, an attempt was made to limit gillnet effort in the northern part of the province by allocating "boat ratings" to specific areas. These boat ratings were based on historic gear levels and average landings. They were altered in later years to encourage more white settlers in the north and to reduce involvement of people of Japanese background in the fishery (Carrothers 1941). Although sockeye salmon were the principal target during the early development of the Skeena fishery, all species of salmon were fished commercially by 1920.

Conservation requirements and overexploitation by the commercial fishery were first expressed as concerns by federal fisheries inspectors in 1916 when the Babine Lake Indians were unable to obtain sufficient sockeye for their winter food supply (Department of the Naval Servie 1917). Over the next 25 years, both the up-river and outer commercial boundaries were gradually moved seaward (Milne 1955). In-season decisions on fishing time and area were not made during this period for a number of reasons:

1) in-season data collection capabilities were limited,
2) weather greatly affected fishing efficiency and hence catch per unit of effort data were suspect,
3) canneries sought a steady supply of fresh raw materials rather than a pulsed supply,
4) announcements of openings and closures could not be communicated to the fleet on short notice.

Throughout this pre-research period, only minor changes were made in the weekly closed time (from 36 to 48 h) and in gillnet mesh sizes. Quantitative information on Skeena sockeye was limited to catch, expressed in cases of canned salmon, with only qualitative estimates of escapement (e.g., poor, average, excellent). The next period in Skeena salmon management corrected most of these data limitations and paved the way for a more scientific approach to salmon management.

RESEARCH PERIOD (1943 TO 1971)

The work of the Fisheries Research Board of Canada was a dominant force in the management of Skeena sockeye salmon during this period. Beginning in 1943, an intensive exploration of all Skeena sockeye producing systems was conducted by the Fisheries Research Board of Canada (Pritchard 1949). The actual numbers of spawners in all spawning areas were estimated for the first time and in 1946 a permanent counting fence was completed on the Babine River (Aro 1961). In the summer of 1951, a disastrous slide on the Babine River resulted in severe reductions of escapements for two successive years. In response to this calamity, the Minister of Fisheries created the Skeena River Salmon Management Committee in 1955. The mandate of this Committee was to restore and, if possible, increase the production of sockeye salmon from the Skeena. The Committee, which consisted of the Chief Supervisor of Fisheries for the Pacific Area and the Director of the Fisheries Research Board was supported by an Advisory Board composed of industry representatives. One of the Committee's first initiatives was to establish a gillnet test fishery immediately upstream from the commercial fishery (Skeena River Salmon Management Committee Annual Report, 1955). Calibrated against the Babine River fence count of sockeye spawners, this test fishery provided a daily estimate of sockeye escapement and formed the basis for a rational in-season management system. Weekly closed times were varied according to fish abundance and weekly escapement target. Extensive limnological work on Babine Lake in the late 1950's and early 1960's (Johnson 1956, 1958, 1961) identified an untapped plankton food supply that could support many more sockeye fry than were being naturally produced. Spawning channels with partial control of water flow and temperature were constructed at Pinkut Creek and Fulton River beginning in the mid-sixties to bolster the fry output to the lake and take advantage of the food reserve. Smolt output has increased substantially since that time (West 1978) and stocks of the Pinkut and Fulton system have shown a steady increase since the late 1970's. Major accomplishments during this research phase can be summarized as follows:

1) development of a maximum sustained yield escapement target for Skeena sockeye,
2) the establishment of adult and smolt enumeration programs at the outlet of Babine Lake,
3) the development of a gillnet test fishery above the commercial fishery to provide in-season estimates of escapement,
4) the discovery that Babine Lake was being underutilized by sockeye fry and the construction of spawning channels to bolster fry production.

CURRENT PERIOD (1972-PRESENT)

The transition from the "Research Period" to the current period began in the late 1960's and was characterized by the transfer of most Skeena stock management responsibilities from the Fisheries Research Board to the stock management sector of the Department of Fisheries. By 1972, fishery managers were responsible for all aspects of Skeena salmon management including the spawning channels, the Babine River adult and smolt counts, and the regulation of the commercial fisheries on the approaches to the Skeena River. Run size still fluctuates widely but has been above earlier averages. Spawning escapement levels indicate that much of the increased production has originated from the spawning channels while stocks have generally declined.

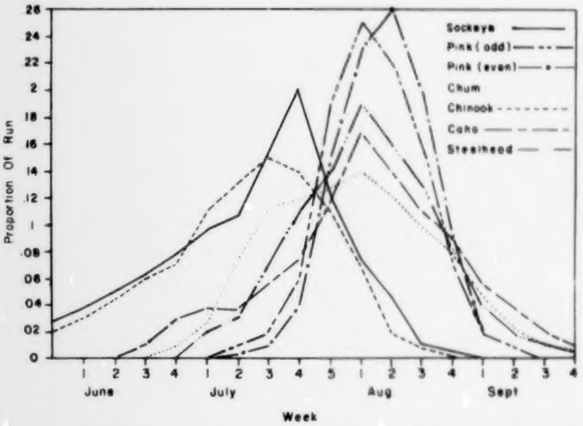


FIG. 2. Proportional run timing of anadromous salmonids through the Skeena River commercial fishery (from unpublished stock timing model, British Columbia Ministry of the Environment, Fish and Wildlife Branch, Vancouver, B.C.)

Probably the outstanding feature of the current management period has been the attention directed toward the mixed stock fisheries problem. The Skeena River chinook salmon and steelhead trout stocks, having migration timing that overlaps with that of sockeye (Fig. 2) (DFO 1985), have experienced very high exploitation rates during sockeye fisheries. In some years Skeena escapements of these species are believed by fishery managers to be well below levels that would maximize production. Although many stocks have been simultaneously harvested in the Skeena sockeye fishery since the start of the commercial fishery, only in the last decade or so have declines in the escapement of incidentally caught stocks been of serious concern to fishery managers. This concern has been echoed, and in some cases initiated, by freshwater sportfishermen and the British Columbia Fish and Wildlife Branch, the agency responsible for steelhead trout management. Management measures taken to alleviate this problem include delaying the start of all net fisheries aimed primarily at harvesting chinook salmon, restricting gillnet mesh size, and closing subareas where the chinook and steelhead catches are high.

Concurrent with the mixed stock problem has been the increasing demands of fishing groups having highly divergent views and preferences on where, how, and by whom Skeena salmon should be caught. This has created considerable pressure on the fishery managers when formulating fishing plans.

Consultation with fishing groups has been recognized as an important step in the preparation of management strategies and fishing plans. However, for an effective fishing plan to emerge, all user groups must understand Skeena stock management objectives and work toward agreement on harvest strategy. Once the fishery begins, managers must make harvesting decisions that are consistent with the guidelines established in the pre-season consultations. This process has been pursued in the Skeena sockeye fishery since the mid-fifties but with mixed results.

Skeena River Salmonid Stocks

Five Pacific salmon (*Oncorhynchus* spp.) and one species of anadromous trout (steelhead, *Salmo gairdneri*) spawn in the Skeena River. Pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon are the most numerous, followed in order of abundance by coho (*O. kisutch*), chinook (*O. tschawytscha*), and chum (*O. keta*) (DFO 1985). Annual returns of sockeye (1951-1984) range from 1 to 3 million, of which 0.2 to 2 million are harvested. Sockeye spawn in more than 50 lakes, rivers, and streams (Hancock et al. 1983a, 1983b) throughtout the Skeena River watershed. The Babine Lake system is the most important sockeye producer with 90% or more of the spawners (Hancock et al. 1983a, 1983b).

Two management agencies in British Columbia and indirectly one agency in Alaska are involved in the fisheries. The Federal Department of Fisheries and Oceans has responsibility for managing all salmon fisheries in British Columbia. However, responsibility for steelhead rests with the Fisheries Branch of the Province of B.C. (British North America Act 1964). Since the majority of returning Skeena steelhead are caught in the sockeye fishery, federal and provincial agencies must cooperate in managing both steelhead and sockeye stocks. Skeena sockeye are also intercepted in southeast Alaskan fisheries managed by the Alaska Department of Fish and Game. Thus, the U.S. agency's management actions also affect catch, and thus achievement of the objectives of the domestic management agencies in B.C.

The escapement timing of the several species overlaps to varying degrees (see Fig. 2). However, Fig. 2 oversimplifies the situation. In reality, each species curve is comprised of a number of stocks, which may have different life-history characteristics such as migration route and timing and age at maturity. With the exception of the earliest and latest stocks, and given the constraints on fishing techniques and locations, fishery managers have little flexibility in manipulating the timing of fisheries to avoid harvesting non-target stocks.

For management purposes, three sockeye stock aggregates are recognized based on run timing (DFO 1985). The early stocks are primarily destined for the Lakelse and Alastair lake systems, the Nanika River, and small tributaries to Babine Lake. These stocks peak in abundance in the commercial fishing area in late June prior to the start of the commerical fishery in most years. The early run stocks currently constitute about 10% of the Skeena escapement.

The middle timed stock aggregate includes Pinkut, Fulton, and Morrison stocks on Babine Lake. Their peak abundance occurs in mid-July but they dominate the fishery until the end of July. Both Pinkut and Fulton stocks are enhanced by controlled flow spawning channels which were phased into production over the period from the mid 1960's to the early 1970's (McDonald and Hume 1984). The current capacity of the two channels is 200 000 spawners.

The late timed aggregate includes the Babine River and Babine lake spawning stocks which peak in late July or early Augut.

Fisheries

Three principal fishing groups harvest Skeena River salmon: commercial (gillnet, seine, and troll), sport, and Indian fishermen. Commercial catches occur in eight fishing areas in northern B.C. and southeast Alaska (Fig. 1). The major fishery is conducted in B.C. Statistical Area 4 with smaller fisheries occurring in Areas 3, 5, and 1. In southeast Alaska, Skeena sockeye are primarily intercepted in the Cape Fox and Sumner Strait gillnet fisheries, and the Clarence Strait and Noyes Island seine fisheries (Gazey, unpubl. MS 1983). Very few sockeye are caught in the Skeena troll and sport fisheries.

Retention of sockeye caught by sport fishermen in non-tidal waters is not permitted under present regulations, while in the tidal area, sockeye comprise a small bycatch in a fishery directed primarily at chinook and coho.

In contrast to the sport fishery, the native Indian food fishery targets on sockeye all the way from the coastal approaches to the Skeena, upstream to some of the spawning grounds. Catches average 100 000 fish but have reached 200 000 in some recent years (Kadowaki et al. 1984).

The Management Process

The step-by-step process of managing salmon fisheries must be capable of defining objectives, implementing strategies for their achievement, and evaluating results. The following two sections outline the annual cycle of Skeena salmon management activities, and in-season procedures for executing fishing plans.

THE ANNUAL PROCESS

Six major components comprise the annual cycle of activities in the management of the Skeena sockeye fishery (Fig. 3).

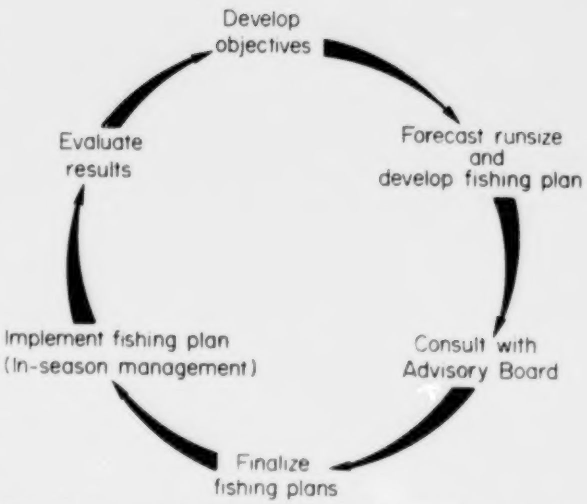

Develop objectives
Forecast runsize and develop fishing plan
Consult with Advisory Board
Finalize fishing plans
Implement fishing plan (In-season management)
Evaluate results

FIG. 3. The annual process for managing the Skeena River sockeye fishery.

Developing objectives

We consider clear management objectives to be essential guidance for those formulating fishing plans. General objectives should give policy direction, while more specific objectives serve as their measurable and practical extensions. For example, the management of fisheries to maximize long-term economic yield is a policy objective, while a target of 900 000 spawners is deemed a measurable specific objective.

The procedure for developing objectives differs from the other components of the fishery management process which are carried out in specified ways and times and linked to the production cycle. Many regional fisheries objectives are developed far from the fishing area, and appear to change very little year to year. This perception can be misleading, however. The priorities assigned to these objectives may change in subtle ways and it is only by examining regulatory actions and through discussions with managers that they are understood.

Within DFO, objectives are developed at the international (Pacific Salmon Treaty 1985), national (Department of Environment 1976, DFO 1982), or regional levels (DFO 1985). In all cases, the primary guiding objectives are the conservation of the resource and the management of stocks to maximize economic and social benefits. However, implementation can vary from arresting the decline in stock diversity (DFO 1982) to ensuring the optimum escapement of all stocks (DFO 1985). Subject to these primary objectives, Indian food fish are the first priority in allocating surpluses. Other objectives are seldom priorized, and some may conflict. Commercial and recreational fisheries are given equal priority after Indian food fisheries and in cases where they compete for the same resource it is not clear how it should be allocated. In another example, the regional 1985 DFO publication of the "Pacific Region Stock Rebuilding Plan" has an overall objective to rebuild salmon stocks (DFO 1985). The lowering of harvest rates in several fisheries is recommended. In the short term, at least, this means less catch, yet it conflicts with another objective from the same report which is to maintain and increase catch in the commerical fishery.

Some of the current objectives driving the Skeena management process can be traced to the early days of the Skeena River Salmon Management Committee. At that time two major objectives guided management actions: (1) rebuild Babine sockeye and (2) maximize the catch. These two objectives eventually culminated in the current escapement target of 0.8 to 0.9 million spawners to the Skeena system. The target was derived from a stock-recruit relationship which suggested the maximum sustainable yield (Shepard and Withler 1958). This escapement target remains one of the few objectives explicitly specified for the Skeena today.

Developing run forecast and fishing plans

There are three methods for forecasting adult returns to the Skeena River: average rate return per spawner, smolt-to-adult survival, and the age 3 to age 4, or age 4 to age 5 ratios. Data from the Babine system are used almost exclusively in forecasting returns. This data set is the most comprehensive of any Skeena sockeye stock and is considered functionally representative of all Skeena stocks since over 90% of the Skeena escapement spawns in the Babine system.

The average rate of return forecast is simply the average number of recruits per spawner for all complete brood years from 1940 to the present. The total spawners for a given brood year are multiplied by this average rate of return to forecast total return. This forecast is then partitioned to the years in which they will return by applying historic age composition data.

Smolt outputs from the Babine system have been estimated by a mark-recapture method since 1961 (Macdonald and Smith 1980). Each year average smolt to adult survival rates are calculated for three periods: all years, most recent 10 years, and most recent 5 years. These values are multiplied by the brood year smolt output to generate a series of run forecasts which are then assigned to the appropriate return year as described above.

The age 3 to age 4 relationship or "sibling" method uses a linear regression to predict age 4 return from age 3 siblings in the previous year. The age 4 to age 5 relationship, conceptually similar to the above, predicts the age 5 return from its age 4 siblings in the previous year. However, instead of using a linear regression relationship, the ratio of the number of age 5 to its age 4 siblings is calculated for all years from 1940 to the present. The average age 5 to age 4 ratio is multiplied by the number of age 4 fish in the previous year to forecast age 5 fish in the current year.

Using the above methods, estimates for each year's return at age 4 and 5 are generated, frequently with wide variability between estimates. A best estimate is chosen by comparing the predicitions using the various forecasting methods with actual returns in past years. This is a subjective process which should be refined analytically.

Given the pre-season run forecast and specific objectives, formulation of the fishing plan is fairly simple. The number of days fishing each week is calculated using historical data to estimate the relationship between run size, effort, e.g., fleet size, and exploitation rate. Since there is no effective means at present of predicting variations in run timing, average timing is assumed. The managers prepare a preliminary report outlining the pre-season forecast and tentative fishing plans. This is distributed to representatives of various interest groups for comments prior to finalizing fishing plans.

Consulting with user groups

The Skeena River Salmon Management Committee remains as the major forum user group input into the management of the Skeena River Fisheries. The Committee, chaired by DFO, is comprised of members from the commercial, sport, and Indian food fisheries. Members are selected by their respective organizations, usually on the basis of knowledge, experience, and gear type affiliation.

The terms of reference of the present Committee are not defined. In practice the Committee advises on the management and enhancement of salmon stocks within the Skeena and adjacent fishing areas. Final authority for management decisions rests with DFO. The committee usually meets two or three times annually: post fishing season (November to December) to review results and give first consideration to plans for the next year's fishery; pre-fishing season (February) to complete fishing plans, and finally; in the fishing season (e.g., second to third week of July) to confirm the expected fishing plan based on an initial assessment of the run size.

Finalizing fishing plans

Following advice from the Committee, fishery managers may modify proposed fishing plans. However, it is often quite difficult to synthesize and apply the advice. Consensus among interest groups on major allocative and other issues is rare, and no formal method has yet been devised to assign weights or values to varied or conflicting advice. Additional factors, such as the catch of Skeena stocks in fisheries which are outside the control of the Committee, such as in southeast Alaska, further confound the development of fishing plans. In any event, managers evaluate the advice as fully as possible before settling on a final fishing plan.

Implementing decisions (in-season management)

In-season management is the process by which actions are implemented during the fishing season to meet the pre-season objectives. It is an iterative decision making process which includes monitoring catch and escapement and achieving weekly harvest rates by manipulating effort i.e., openings, fishing areas, and gear type. Details of in-season management are reviewed in the next section.

Evaluating results

The primary evaluation performed by fishery managers is to determine the effectiveness of management decisions in achieving desired spawning escapements. All fish entering the Babine Lake system are counted through a fence. A large Babine River population spawns between the counting fence and Babine Lake and is estimated by a mark-recapture program. Of the fish that enter the lake, the majority will spawn in the two enhancement facilities where counting fences permit accurate counts to each. Smaller stocks in tributary streams are enumerated by foot and from the air. Lake spawners, which have comprised up to 30% of the run, are calculated by deducting the total number of fish that enter the lake from the combined numbers estimated in the tributaries, Babine River, and the enhancement facilities. The remaining non-Babine systems are surveyed by foot or air to obtain escapement estimates; the accuracy of these counts is unknown.

Annual escapement data are reviewed with the Skeena Management Committee in a post-season meeting. Deviations from pre-season goals and expectations are analyzed to see what prevented attainment of goals, which assumptions proved untenable, and what corrective actions might be appropriate in the future.

THE IN-SEASON PROCESS

In-season management has four major components: (1) data collection, (2) run assessment, (3) decision-making, and (4) implementation. These are discussed below.

Data collection

This includes the following data and observations to assess run strength, composition, and timing.

i) Test fishery

The gillnet test fishery provides a daily in-season estimate of sockeye and pink salmon escaping the fishery into the Skeena River. Fish usually require only a single day to travel from the fishery to the commercial fishing boundary, thus making the test fishery a very effective management tool. Catch per hour indices are regressed against counts at the Babine fence. This has been done over many years to produce the predictive relationship. This relationship is particularly reliable for sockeye because of their predominantly Babine River origin. Despite this high quality calibration, the error in the in-season escapement estimate in recent years has averaged 15% in the period from 1979 to 1984 (Fig. 4). A correction factor accounting for variability in annual mean fish length was incorporated into the relationship prior to the 1985 fishing season (Kadowaki 1985, unpubl. MS). This significantly improved the 1985 estimate (L. Jantz, DFO Prince Rupert, pers. comm.).

ii) Commercial catch

Commercial catches are a second important source of data on run strength and timing. Estimates are made by fishery officers using catch per unit effort (CPUE) and effort (i.e., boat day or set) from the fishing grounds. Catch and CPUE from Area 4, the commerical fishing area closest to the Skeena River, provides the most useful information, while catches from more distant fisheries require more careful interpretation due to uncertainty over constituent stock timing and composition and Skeena sockeye migration routes. For example, although the seine fishery at Noyes Island in southeast Alaska catches significant numbers of Skeena sockeye (Gazey 1983) their proportion in the fishery is likely quite variable. CPUE data in distant fisheries is therefore of little value to the in-season process.

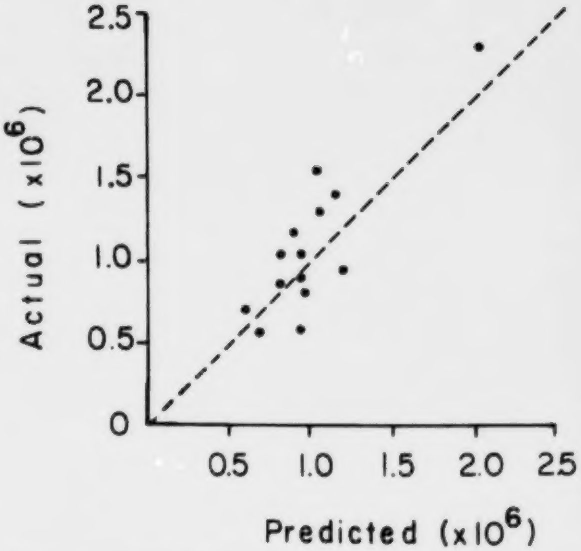


FIG. 4. Actual versus predicted escapements by the Skeena River test fishery 1970–85 (from unpublished data files of the Department of Fisheries and Oceans, Prince Rupert, B.C.).

iii) Indian food fishery

The coastal waters Indian food fishery occurs during commecial fishery closures. It can be a useful information source but requires careful interpretation. The fleet of 10 to 40 Indian vessels can attain very high CPUE's on medium-sized runs since they have unhindered access to preferred fishing areas. They also usually fish on preferred tides causing further inflation of CPUE estimates.

iv) Biological sampling

The test fishery and commercial catches are sampled for age, size, and sex composition. These attributes are most important in post-season assessment and pre-season forecasting, but they also provide in-season clues to the strenght and timing of the run to come. For example, age 5 sockeye almost always have have an earlier mean date of return than age 4's and males tend to have an earlier mean date of return than females (Withler 1945). Further analysis is required before the reliability of these tendencies can be quantified.

v) Environmental variables

All catch data must be interpreted in terms of environmental factors. Tide height and stage, wind speed and direction, sunlight, and rainfall can all affect catchability. General trends in climatic and oceanographic conditons probably constitute significant influences but have not yet been factored into our analyses.

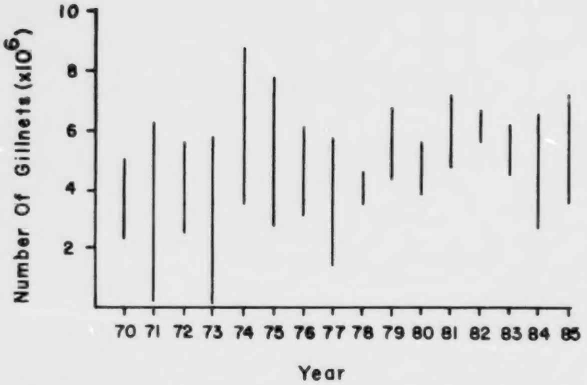


FIG. 5. Range of daily gillnet fleet size for July, 1970–85 (from unpublished data files of the Department of Fisheries and Oceans, Prince Rupert, B.C.).

vi) Fleet size and distribution

Fleet size can vary greatly (Fig. 5). Good fishing in other areas can draw boats away while poor fishing or closures elsewhere could divert them to the Skeena. Increases in gear generally lead to higher exploitation rates and must be taken into account when setting fishing times. The impacts of fleet distribution are evaluated subjectively based upon the experience of fishery managers and their knowledge of historical response patterns.

Fishery managers weight the data from all these sources to assist them in making in-season management decisions (Table 1).

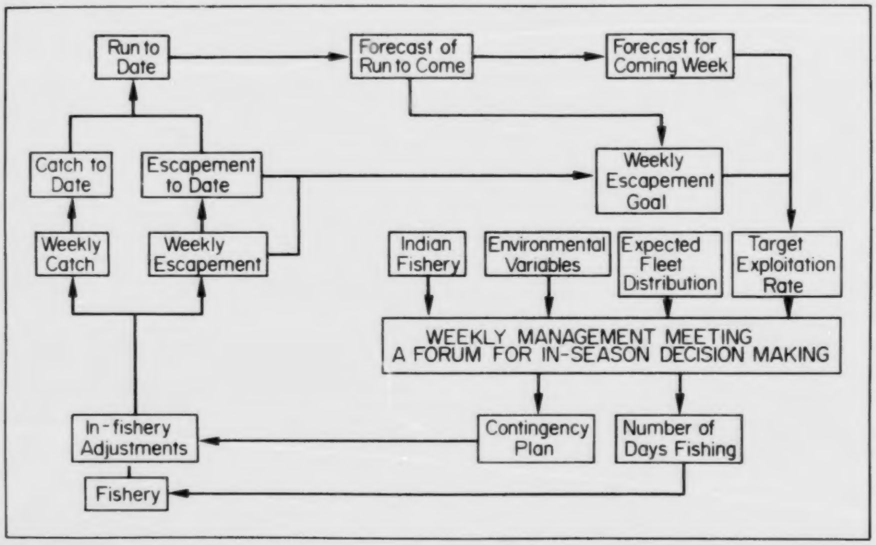
TABLE 1. Information inputs and their priority and uncertainty for in-season management as determined by fishery managers.

Input	Priority	Uncertainty
Test fishery	high	low
Commercial catch	high	low
Indian food catch	low	high
Biological sampling	low	high
Environmental variables	moderate	moderate
Fleet distribution	moderate	moderate

Run assessment

Fisheries managers carefully monitor the runs as they progress and when needed they modify expectations and fishing plans accordingly. A fishery management model (Fig. 6) similar to the one proposed by Walters and Buckingham (1975) represents the in-season control system for predicting run size and evaluating the impacts of alternate harvest strategies on catch and escapement. The model utilizes an iterative process which uses catch and escapement from the current week to forecast fishing effort and run size for the next week and the total run to come. The variances of the pre-season and in-season run estimates are weighted to minimize the variance of the total run estimate. The accuracy of the pre-season forecast is highly variable (Fig. 7) and once in-season information is available the pre-season estimate becomes progressively less important (Fig. 8).

The weekly escapement target proposed in the pre-season fishing plan is also modified at intervals after the season



Run to Date
Forecast of Run to Come
Forecast for Coming Week
Catch to Date
Escapement to Date
Weekly Escapement Goal
Weekly Catch
Weekly Escapement
Indian Fishery
Environmental Variables
Expected Fleet Distribution
Target Exploitation Rate
WEEKLY MANAGEMENT MEETING A FORUM FOR IN-SEASON DECISION MAKING
In-fishery Adjustments
Contingency Plan
Number of Days Fishing
Fishery

FIG. 6. The in-season management process for the Skeena River sockeye fishery.

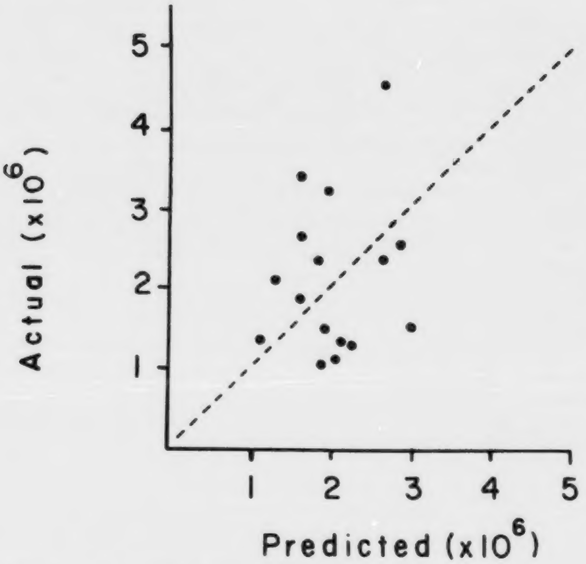


FIG. 7. Actual versus forecasted (pre-season) run sizes of Skeena sockeye 1970–85 (from unpublished data files of the Department of Fisheries and Oceans, Prince Rupert, B.C.).

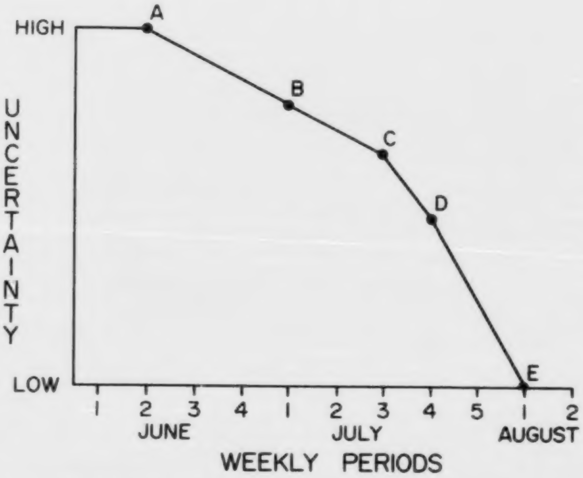


FIG. 8. Run size uncertainty in the in-season management of Skeena River sockeye: A — test fishery begins, B — commercial fishery begins, c — peak of run observed, D — peak confirmed, E — most of run accounted for.

begins according to the escapement to date and the run still expected. In years of large returns (>2.0 million), and assuming a 4 day per week fishery, this modification is designed to maintain weekly harvest rates at no more than 60%. This ensures that some of the less productive stocks are maintained although not necessarily at maximum sustained yield levels.

The in-season decision making process is driven by the rate of fishery exploitation required to produce the desired spawning escapement. Measurement error and uncertainties in the relationships between indices and actual abundance fuel discussion in the decision making step.

Decision-making

Deciding when and how long to allow fishing is very difficult, and managers are typically faced with a variety of uncertain biological and non-biological data on which to base their decision. On the Skeena, a group decision-making process attempts to reconcile uncertainties and evaluate the various inputs to arrive at the best decision.

Management meetings are held almost daily and are attended by key DFO personnel (Table 2) to: (1) decide on the fishing pattern for the following week and (2) determine if in-fishery adjustments to seasonal plans are warranted.

TABLE 2. Participants and their roles in the in-season decision-making process.

Participant	Role
1) District supervisor	— the senior fishery officer in the District, acts as chairman.
2) Sub-district officer	— fishery officer in charge of the fishing area, has the legal authority to regulate fisheries and is usually most familiar with the actual prosecution of the fishery. He provides data on current and historical catch and effort patterns.
3) Management biologist	— an advisor to the fishery officer, responsible for stock and fishery assessment. This involves the analysis of catch and escapement data and projections of the run to come.
4) Senior management biologist	— ensure consistency in stock and fishery assessment between fishing areas. Not always present at routine management meetings but is usually present for critical and very difficult decisions to lend his experience and expertise.
5) Area manager	— has final authority at the field level for all fishing plans. Attends crucial meetings but reviews all decisions before they are implemented to ensure consistency with objectives.

Prior to the meeting each participant decides how much weight should be assigned to specific factors. The fishery officer and management biologist outline their initial position as to the appropriate management decision and explain their rationale for the relative weights they have assigned to the available information. Colleagues discuss these positions and may offer views of their own. More discussion occurs if the positions and the emphases differ. Differences are likely to occur because: (1) regional objectives are open to differing interpretations, (2) there are contrasting perspectives on acceptable risk, (3) there are differing gear expections, and so on. This discussion usually produces a decision supported by all participants. It is very much like a negotiation but rather than being adversative, it usually brings cooperating individuals to a shared decision.

Implementation (regulatory action)

Fishery officers promulgate regulations for the commercial, sport, and Indian fisheries and are responsible for directing and enforcing in-season management decisions. Their major regulatory tools are fishing time, area, and gear. The commercial fishing areas are subdivided into management units and, under the authority of the fishery officers, they are opened and closed to regulate the fisheries. Typically, fishing areas are open for a specified gear type and time. For instance, net and troll gear openings generally vary from 24 to 96 h weekly, over an 8-wk period. However, in offshore fishing areas trolling may continue 7 days per week until a season ending date or a catch ceiling is reached. Sport fish regulations are usually developed a year in advance and seldom adjusted. The Indian food fishery is regulated by permits which prescribe gear, area, and time. In the coastal area they are issued for specified days throughout the fishing season upon request.

Discussion

Effective in-season Skeena fishery management requires well defined objectives specified in advance, and rapid digestion and sythesis of a broad spectrum of emerging information. If this process operates well, good decisions on fishing gear, times, and areas can, and usually do result. Conversely, if objectives are vague and data are incomplete or uncertain, it becomes difficult or impossible to create an effective regulatory regime. For instance, in recent years unclear harvesting priorities and uncertain test fishery interpretations have resulted in underexploitation of sockeye produced in the Babine enhancement facilities. Thus, significant harvests were foregone. We also believe that rigid adherence to traditional fishing methods have at times contributed to overexploitation of several less resilient stocks (Kadowaki et al. 1984).

DEFINING OBJECTIVES

The Advisory Committee on Marine Research and Resources (ACMRR 1980) stressed the importance of considering fisheries management as a coordinated system which progresses logically from defining objectives to evaluating results. A prominent feature of Skeena River sockeye management (and Pacific salmon fisheries management, in general) is a hierarchical structure for decision-making (Peterman et al. 1978). Consequently, it should be possible to trace historic in-season management decisions back through the decision-making process to the pre-season objectives which generated them and learn more of past decision-making. Unfortunately, the linkages are often found to be tenuous or unclear, suggesting that no specific objectives existed. In the absence of this historic information, and the vagueness of some contemporary objectives, it has been enormously difficult to settle on the most appropriate management actions, and the chances of making poor decisions and putting the stocks at risk are greatly increased.

Objectives which have been documented have not always been explicit or priorized so most suitable management responses can only be generally inferred from past records and experiences. This frustrates managers and exacerbates difficulties in reconciling multiple objectives, many of which conflict (Peterman et al. 1978).

Multi-attribute utility theory (MAUT) has been suggested as an objective and quantitative technique to resolve multiple objective problems such as those on the Skeena. Walters and Hilborn (1977) and Keeney (1977) applied this technique to evaluate multiple objectives of the Skeena River salmon fishery. The results, as noted by Healey (1984), did not attract much attention from fishery managers. This could be partly due to the preliminary nature of the findings, but a more serious problem may be uncertainty of some user groups as to the rationale and wisdom of particular management objectives. In any event, when the objectives are clearly outlined and carefully priorized, the fishery managers decision making should be relatively straight forward.

Ideally, explicit and priorized biological and social management policy objectives would be reached through cooperative DFO user group dialogue. Once in place, local management, with input from local users, could move directly to the required specific objectives.

COPING WITH UNCERTAINTIES

Biological uncertainty is a most pervasive factor in fisheries management, and effectiveness in dealing with this uncertainty and making suitable harvesting decisions is one measure of management's success. Sissenwine (1981) has suggested various methods of minimizing uncertainty, and such actions as improving stock abundance models and designing efficient fishing regimes should be done where possible.

Uncertainty which arises because of unknown fleet size, test fishery performance, or dubious pre-season forecasting obviously compounds management difficulty and heightens risk to the stocks. In our experience, the weekly management meeting provides the best forum for discussing the uncertainties and assessing the risk associated with various courses of action.

The management meetings necessarily involve a good deal of subjective rather than analytical decision making. For example, in recent years the test fishery has consistently underestimated the sockeye escapement. Prior to 1985, this was thought to result because fish were becoming smaller and fewer were being caught in the test net. This subjective reasoning caused managers to lose faith in the test fishing estimates in favor of such measures as total catch and CPUE. In 1985, the suspected relationship between fish size and test net catches was proven and quantified and the test fishery immediately regained its earlier favor as a prime management tool.

Since participants in the management meeting are likely to assign different levels of uncertainty and accept different levels of risk in situations, we believe that our "negotiation process" is an important factor in reaching satisfactory conclusions. In particular, it seemed effective in achieving both social or allocative, and escapement goals. It could, however, be strengthened further and made more understandable to user groups and interested managers elsewhere. Required is an explicit statement of the criteria used in making management decisions, and rigorous documentation of both analytical and subjective judgements (Wilimovsky 1985). Predicted and actual outcomes can then be compared and the performance of the decision-making process evaluated and fine tuned. This would be similar to the "clock work" management approach currently used in the Johnstone Strait chum fishery (Johnstone Strait-Fraser River Chum Advisors 1985, Nanaimo, B.C. unpublished). This plan sets rules on a weekly basis which are agreed to prior to the season and which drive the decision making process.

Conclusion

Management of the Skeena River sockeye fishery has evolved into an intricate hierarchical decision-making structure. A group decision-making process usually copes effectively with uncertainties when making in-season decisions. Defining the set of decision criteria and documenting value judgements would improve the process. The lack of explicit objectives and goals, however, inhibits the analysis of management alternatives and impedes the evaluation of management performance. A detailed "clock-work" management plan could be used to document decision criteria and make the process more understandable to fishing groups.

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Recommendation for Rational Exploitation of Sockeye Salmon (*Oncorhynchus nerka*) from the Kamchatka River

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Abstract

BUGAEV, V. F. 1987. Recommendation for rational exploitation of sockeye salmon (*Oncorhynchus nerka*) from the Kamchatka River, p. 396–402. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Sockeye salmon (*Oncorhynchus nerka*) of the Kamchatka River are exploited by intensive Soviet coastal-river and Japanese high seas fisheries. Total returns to the principal stocks or groups of sub-stocks were estimated for the years 1955–1983 using Soviet catch data and an index of interception by the Japanese high seas fishery. For most stocks, recruitment was correlated with air temperature during egg incubation; this correlation was either positive or negative depending on whether the juveniles reared in deep or shallow lakes. Recruitment in some stocks also increased following the natural fertilization of rearing areas by ash from volcanic eruptions. Spawning escapements appear to be below optimum. Recommendations were made to provide a rational basis for rebuilding important individual sockeye stocks.

Résumé

BUGAEV, V. F. 1987. Recommendation for rational exploitation of sockeye salmon (*Oncorhynchus nerka*) from the Kamchatka River, p. 396–402. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Le saumon nerka (*Oncorhynchus nerka*) du fleuve Kamchatka fait l'objet d'une pêche intensive en milieu côtier et fluvial par les Soviétiques et en haute mer et par les Japonais. Les remontes totales pour les principaux stocks ou groupes des sous-stocks ont été estimées pour les années 1955–1983 à l'aide de données soviétiques sur les prises et d'un indice d'interception par les pêcheurs japonais hauturiers. Pour la plupart des stocks, le recrutement était corrélé à la température de l'air pendant l'incubation des oeufs; cette corrélation était soit positive ou négative selon que les juvéniles vivaient dans des lacs profonds ou peu profonds. Chez certains stocks, le recrutement a aussi augmenté après la fertilisation naturelle des aires de croissance par la cendre provenant d'éruptions volcaniques. L'échappée semble être inférieure au niveau optimum. On présente des recommandations qui serviront de base rationnelle pour le rétablissement d'importants stocks de saumon nerka.

Sockeye salmon of the Kamchatka River are among the most abundant of Asian stocks, and are the object of intensive Soviet coastal-river and Japanese high seas fisheries (Ostroumov 1964; Simonova 1978). Quotas were imposed on Japanese high seas sockeye fishing beginning in 1978. Given the relative escapements of present and former years, the numbers of Kamchatka sockeye salmon that could be taken by Soviet fisheries in 1978–83 was 1.6–2.5 thousand t.

In spite of generally increased populations on the spawning grounds, escapements to individual tributaries of the Kamchatka River basin have been irregular. Even in recent years, many escapements have been only 10–15% of those prior to the intensive Japanese high seas fisheries, and some of the smaller spawning populations have disappeared. There can be little doubt that this resulted from prolonged overexploitation of Kamchatka sockeye stocks by the Japanese high seas fishery. The disappearance of some small populations suggests that the genetic diversity of Kamchatka sockeye may have been reduced.

In this paper, I discuss possibilities for more rational exploitation of Kamchatka sockeye by domestic fisheries, taking into consideration the different life histories of individual stocks and groups of sub-stocks in the watershed of the river (Bugaev 1983a, b). I assume that rational, scientific management will contribute to an increase in production by these stocks.

Materials and Methods

At present, it is possible to differentiate among fish of the following stocks and groups of sub-stocks of sockeye salmon (Bugaev 1987) (Fig. 1):

1) A group of sub-stocks from the tributaries of the upper and middle reaches of the Kamchatka River (Bugaev 1984a) whose fry migrate to sea as age 0. fingerlings ("*S*" group).

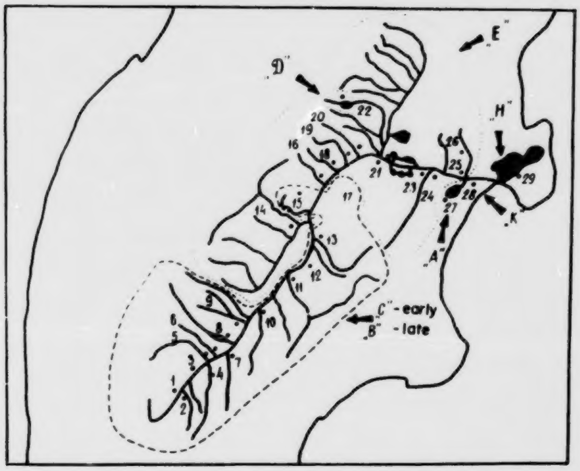

FIG. 1. Sockeye spawning areas in the Kamchatka River basin: 1 — Puschino village, 2 — Kashkan river, 3 — Sharoma village, 4 — Kavycha River, 5 — Andrianovka River, 6 — Zhupanka River, 7 — Vakhvina River (Valagina), 8 — Kirganik River, 9 — Kimitina River, 10 — Kitilgina River, 11 — Shchapina River, 12 — Nikolka River springs, 13 — Tolbachik River, 14 — Bystraya-Kozyrevka River, 15 — Shekhlun River, 16 — Kreruk River, 17 — Ushkovskoe Lake springs, 18 — Kryuki River, 19 — Polovichnaya River, 20 — Belaya River, 21 — Yelovka River, 22 — Dvukhyurtochnoe Lake, 23 — Bolshaya Khapitsa River, 24 — Malaya Khapitsa River, 25 — Raduga River, 26 — Nizovtsevo Lake (basin of the Raduga River), 27 — Azabachye Lake 28 — Kursin Lake, 29 — Soldatskaya River (basin of the Nerpichye Lake).

Ed. Note: Group symbols "*B*", "*C*", and "*H*" are transliterated in text as *V*, *S*, and *N*, respectively.

2) A group of sub-stocks from the tributaries of the upper and middle reaches of the Kamchatka River whose fry rear in the river near the spawning grounds before migrating to sea as age 1. smolts ("*V*" group).

3) A group of sub-stocks from the tributaries of the lower and middle reaches of the Kamchatka River (Bugaev 1981, 1982) whose fry rear in Azabachye Lake before migrating to sea as age 1. smolts ("*E*" group).

4) A stock spawning in Azabachye Lake (Bugaev 1983c) whose fry rear in the lake together with the juveniles of group "E" before emigrating to sea as age 2. smolts ("*A*" stock).

5) A stock whose fry rear in Dvukhyurtochnoe Lake before emigrating to sea as age 2. smolts ("*D*" stock).

6) A stock whose fry rear in the brackish-water Nerpichye Lake before emigrating to sea as age 1. smolts ("*N*" group). This group also includes sub-stocks from lower tributaries of the Kamchatka River whose young migrate to Nerpichye Lake where they forage and spend one winter before emigrating to sea (Bugaev 1984b). I was unable to differentiate sockeye from the Nerpichye Lake stock from the latter group of sub-stocks when caught in the fishery.

7) A stock whose fry rear in the Kursin Lake watershed before emigrating to sea as age 1. smolts ("*K*" stock).

All of these stocks and one group of sub-stocks comprise both early (spring) and late (summer) seasonal races ("*E*", "*A*", "*D*", "*K*", "*N*") but the other groups ("*S*", "*V*") comprise only one seasonal race. Group "*S*" is an early run whereas group "*V*" is a late one, but both spawn in the same general area. In the following analysis, age at maturity was assumed to be 0.3 for group "*S*", 1.3 for groups "*E*", "*V*" and "*N*", and 2.3 for stocks "*A*" and "*D*"; stock "*K*" was not considered since it is not abundant.

The Soviet catch of these seven groups of Kamchatka sockeye has been estimated annually since 1978 using differences in scale patterns; Soviet catches from 1957 to 1977 were also estimated by extrapolation from recent figures. Although it is possible to recognize some Kamchatka sockeye stocks in catches from the Japanese high seas fishery (Konovalov 1971), stock identification techniques are not sufficiently reliable to estimate the actual composition of Japanese catches. Accordingly, a rough index to the Japanese catch of Kamchatka sockeye has been developed based on the ratio of the annual Japanese high seas catch to the average annual Japanese high seas catch during 1978–83. Deviations from the average in the Japanese catch are attributed to proportional deviations from the average return of Kamchatka sockeye. Thus,

$$N_I = \frac{N\ C}{(1-u)\ \bar{C}}$$

where N_I is an index of total abundance and N is the observed escapement of Kamchatka sockeye (or a group of Kamchatka sockeye), $\bar{C}$ is the average annual catch by the Japanese high seas fishery during 1978–83, C is the annual catch for the year in question, and u is the annual rate of exploitation by Soviet fisheries.

Results

Bugaev (1983a) investigated the effect of thermal regimes in the Kamchatka River watershed on sockeye salmon recruitment. Study years were classified as "warm" or "cold" according to whether temperatures during the warmest (June–August) period of the year were higher or lower than the long-term average (10.1°C). The strongest correlations were usually between numbers of returning adults and air temperature at Ust-Kamchatsk settlement during early egg incubation; returns were not correlated with temperatures during winter egg incubation, alevin and fry development, or fingerling growth in summer. In cold years, groups "*S*", "*E*", and "*N*" were favoured; the juveniles of these groups rear in shallow lakes and sidechannels (groups "*S*" and "*E*"), or in the brackish-water Nerpichye Lake (group "*N*") for a period of time, after migration from the spawning grounds. On the other hand, in warm years, stocks "*A*" and "*D*" were favoured; juveniles from these stocks rear in large, deep lakes. Summer incubation temperatures were not correlated with recruitment of group "*V*", the fry of which rear near the parental spawning areas in their first summer (Bugaev 1983a).

In addition to temperature effects on production, Azabachye Lake sockeye salmon may have been affected by fertilization of the lake by ash resulting from volcanic eruptions. Kurenkov (1975), for example, concluded that ash from an eruption of the Bezymyanny volcano in 1956 greatly enhanced plankton growth in Azabachye Lake and subsequently increased production of the Azabachye Lake sockeye stock. Although "*E*" group juveniles forage in Azabachye Lake before emigrating to sea, production by these sub-stocks depends primarily on annual temperatures and to a lesser ex-

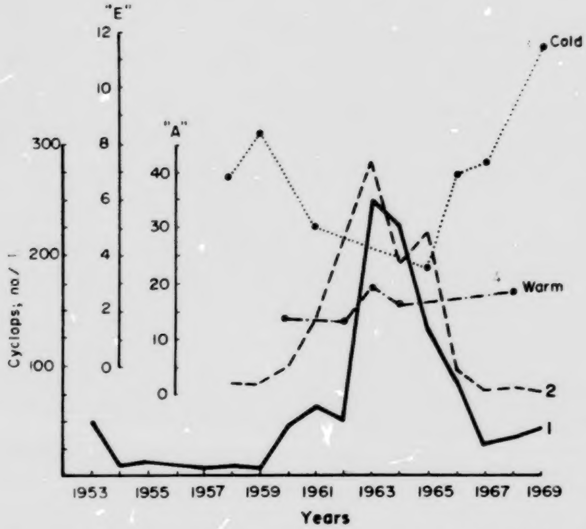

FIG. 2. Rate of return (return/spawner) of sockeye salmon of group "*E*" and stock "*A*" in relation to the density of Cyclopoda in Azabachye Lake.
1- Cyclopoda density in the autumn; 2- production of stock "*A*"; 3- production of group "*E*" in cold years (≤ 10.1 °C); 4- production of group "*E*" in warm years (> 10.1 °C).

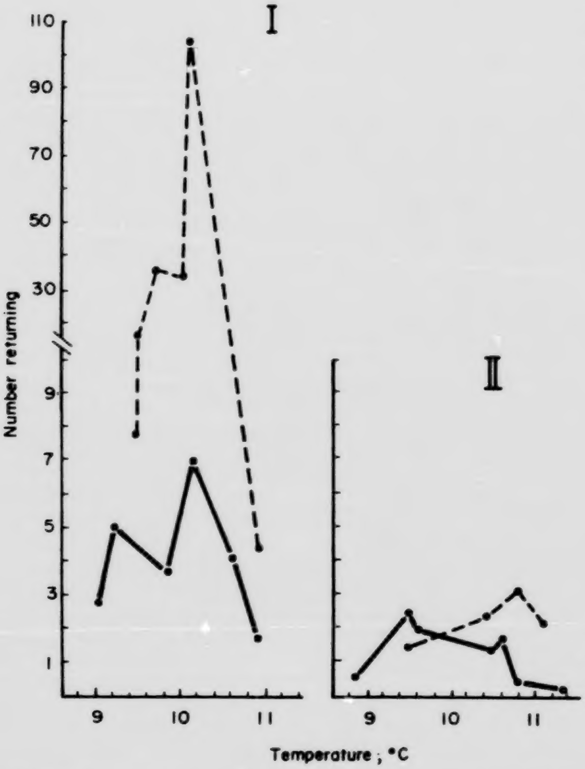

FIG. 3. Rate of return of sockeye salmon of group "*S*" relative to the June–August mean air temperature in Ust-Kamchatsk Settlement. Dashed lines show strength of 1957–66 year-classes in the Kamchatka River following eruption of Bezymyanny volcano. I — small escapements; II — large escapements.

tent on feeding conditions in the lake where the fry are in competition with "*A*" stock (Fig. 2).

Group "*S*" sockeye appear to have been influenced favourably by the 1956 Bezymyanny eruption (Fig. 3). Large amounts of ash fell in the Kamchatka River valley, especially in lakes of the Kamakovskaya lowland during the eruption (Kurenkov 1975; Ostroumov 1984). "*S*" group fingerlings migrate through this area mainly in June (Bugaev and Karpenko 1983; Bugaev 1984a), at a time when a brief plankton bloom takes place in the local lakes (Kurenkov 1967). These factors may explain the increase in returns from years following the eruption. The eruption of the Bezymyanny volcano had considerably less influence on stock "*D*", and groups "*E*", "*V*", and "*N*" whose fry also migrate through the lakes of the Kamakovskaya lowland. This is probably because these juveniles passed through the area later, during July–August, when plankton had already been flushed away by high water (Kurenkov 1967). Moreover, these juveniles would have been much larger at that time (about 50–120 mm) compared to the "*S*" group (about 30 mm), and thus, less affected by environmental conditions (Nikolsky 1974).

We also believe that ash from the eruption of the Tolbachik volcano in 1975 resulted in a considerable increase in production of stock "*A*" from the 1977–78 spawnings. In fact, returns from broods affected by the Tolbachik eruption were probably 2.5–8.6 times higher, and by the Bezymyanny eruption 2.6–12.6 times higher than average. These examples of natural fertilization of Azabachye Lake testify to the desirability of artificial fertilization for this watershed. Stock "*A*" juveniles foraging in the lake without benefit of volcanic fertilization produced below optimum returns; those growing during the period of volcanic fertilization produced high returns, despite considerable variation in spawning escapement.

It is instructive to ask why the 1956 Bezymyanny eruption influenced production of group "*S*" sockeye while the

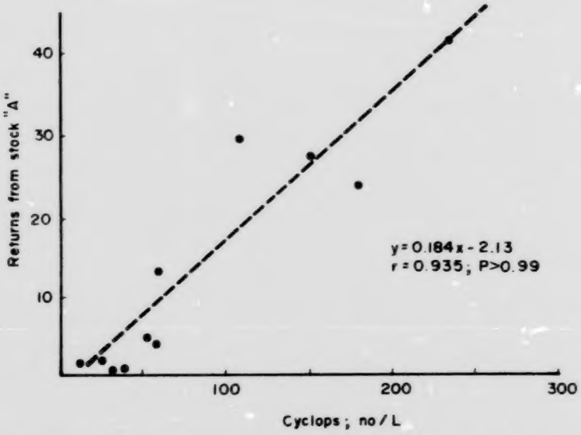

FIG. 4. Relationship between the average abundance of *Cyclops scutifer* (Sars) copepodites in two autumns in Azabachye Lake during residence of juvenile sockeye and subsequent rate of return of adults of stock "*A*".

Ed. Note: Group symbols "*B*", "*C*", and "*H*" are transliterated in text as *V*, *S*, and *N*, respectively.

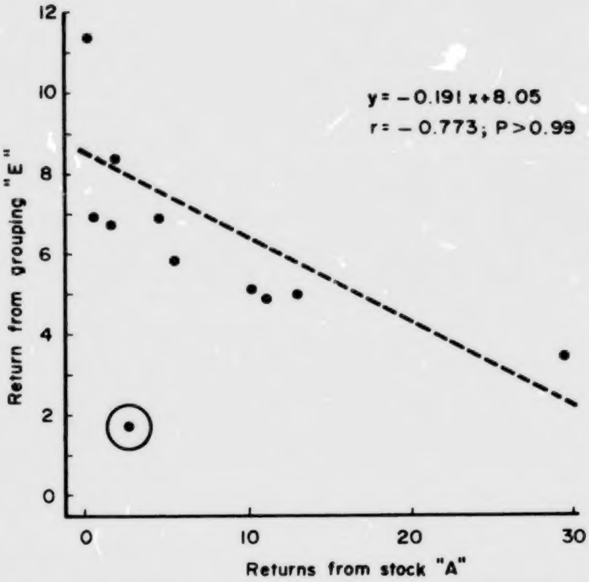

FIG. 5. Relationship of rate of return of stock "*A*" and group "*E*" from cold brood years. Circled year is not included in calculations.

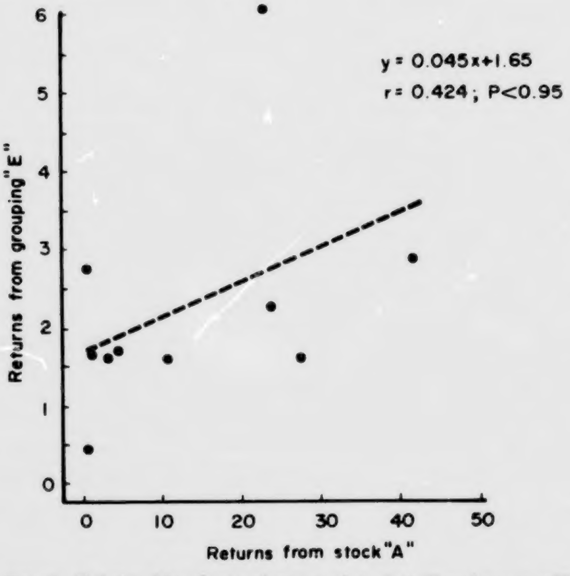

FIG. 6. Relationship of rate of return of stock "*A*" and group "*E*" in warm brood years.

1975 Tolbachik eruption did not affect group "*S*" but did influence stock "*A*". A possible explanation is that the quantity of ash in the Kamchatka River valley in 1956 was considerably greater than in 1975, and the Bezymyanny volcano was closer to the Kamakovskaya lowland than the Tolbachik volcano. While the increase in group "*S*" production was apparent in the first year-classes after the eruption of the Bezymyanny volcano (Fig. 3), the increase in stock "*A*" returns was not apparent until some years later (Kurenkov 1975).

There is a stong positive correlation between the abundance of cyclopoid copepods (the main food of young sockeye salmon) in Azabachye Lake and production of stock "*A*" (Fig. 4). For year-classes rearing during cold years, there is an inverse relationship between production of stock "*A*" and group "*E*", both of which have juveniles foraging in Azabachye Lake (Fig. 5). This relationship probably results from intense competition for food when production in the lake is poor. Production of stock "*A*" and group "*E*" was positively correlated when year-classes foraged together in warm years (Fig. 6).

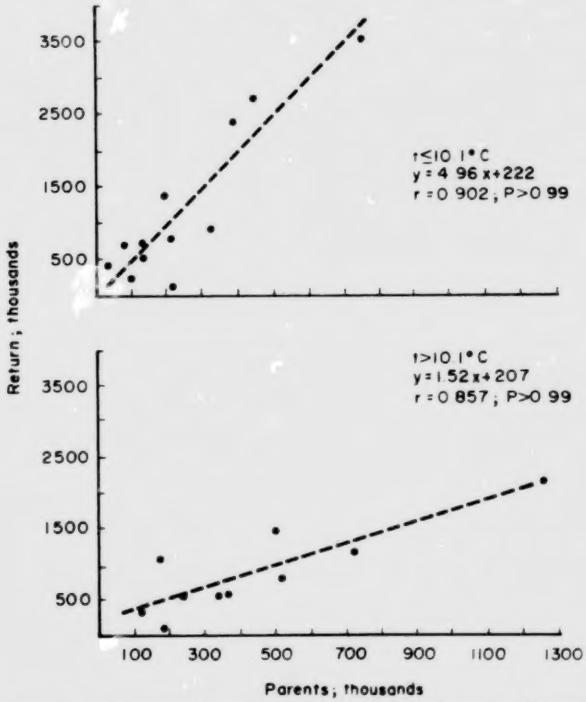

FIG. 7. Spawners and recruitment of sockeye of group "*E*" and "*N*" in cold (top frame) and warm (bottom frame) brood years. Group "*N*" fish comprise 8–9% of the total.

Discussion

To develop a rational plan for exploiting Kamchatka sockeye populations, we must determine the number of spawners required to maximize production of each stock and group.

It is apparent from Fig. 7, that in both cold and warm years, group "*E*" production was directly proportional to spawning escapement which indicates that escapements were below the level at which egg-to-fry survival is diminished. A similar conclusion may be drawn for sockeye of group "*V*" (Fig. 8) and stock "*N*" (Fig. 9). Optimum escapements have already been determined for group "*S*" (except in cold years) and stocks "*A*" and "*D*".

Treating all stocks and groups of sockeye salmon in the Kamchatka system as a unit, we estimated the optimum number of spawners to be 1 400 000 in cold years and 2 025 000 fish in warm years. The estimated total adult pro-

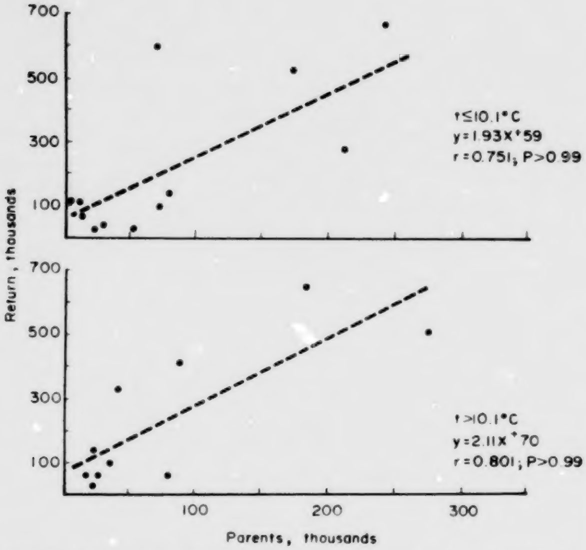

FIG. 8. Spawners and recruitment of sockeye of group "*V*" in cold (top frame) and warm (bottom frame) brood years.

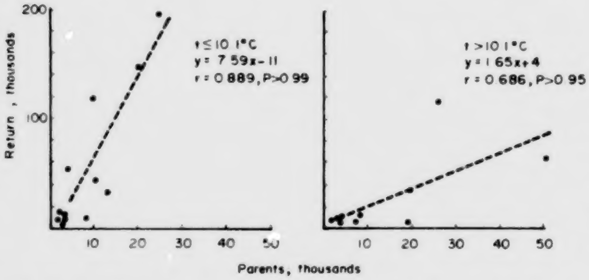

FIG. 9. Spawning and recruitment of sockeye of group "*N*" in cold (left hand frame) and warm (right hand frame) brood years.

duction from such escapements (not including year-classes whose recruitment was affected by eruption of the Bezymyanny and Tolbachik volcanos) is 5 600 000 and 3 580 000 fish for cold and warm years, respectively; of this, 4 200 000 fish (10.5 thousand t) and 1 555 000 fish (3.9 thousand t), respectively, would be available to the Soviet fisheries. The estimated average catch over all years would be 7.2 thousand t which is similar to the actual average catch of Kamchatka River sockeye during 1932–77 of 6.2 thousand t (Ostroumov 1964). Because the yield has been as high as 20 thousand t in the past, the estimated optimum spawning escapement may be underestimated. Spawning escapements have not reached the estimated optimum since 1957, although in some years they came close.

Achieving the optimum escapement, and thereby an increase in yield from Kamchatka River sockeye, is only one approach to rational management. Artificial fertilization of Azabachye Lake should also be considered, since fertilization by volcanic ash appears to have been beneficial. However, volcanic eruptions as large as that of 1956 occur very seldom, and it would be premature to use these data to justify artificial fertilization of the Kamchatka River valley and particularly the lakes of the Kamakovskaya lowland. Specialized investigations would be needed to assess the feasibility of such projects. Furthermore, returns from group "*S*" year-classes affected by the 1975 Tolbachik eruption are still incomplete.

As noted above, there is a direct relationship between Azabachye Lake plankton (*Cyclops scutifer*) abundance and the catch of stock "*A*"; returns were considerably enhanced when the abundance of *C. scutifer* exceeded 50/L. Thus, the abundance of cyclopoid copepods should be maintained above this level. Large escapements of stock "*A*" fish are probably counterproductive since the optimum number of spawners is rather low. Consequently, there is a high risk of over-spawning in the lake basin with commensurate low reproductive success. We must also take into account the undesirable aspects of interaction between juveniles of stock "*A*" and group "*E*".

TABLE 1. The contribution (in %) of local stocks and groups of sockeye salmon in the run to the Kamchatka River in 1978–83.

	Stock or group							
Year	***E***	***A***	***S***	***V***	***N***	***D***	***K***	**Total**
1978	58.1	15.7	9.4	6.8	5.1	4.8	0.1	100.0
1979	47.3	21.0	17.4	5.5	3.0	5.4	0.4	100.0
1980	57.0	21.8	7.7	3.7	4.1	5.4	0.3	100.0
1981	45.8	23.5	14.1	7.4	4.2	4.6	0.4	100.0
1982	47.9	27.1	12.3	5.6	3.4	3.4	0.3	100.0
1983	38.3	32.7	16.4	7.0	2.3	3.1	0.2	100.0

Plans for rational exploitation of Kamchatka river sockeye salmon must include a means of identifying component stocks and groups in mixed-stock fisheries. Fishing can then be regulated in such a way that management objectives for the combined stocks will be achieved. This is essential to achieve optimum escapements of stock "*A*" and groups "*E*" and "*S*", the largest groups in the watershed (Table 1), which sometimes differ in timing (Bugaev 1983b).

Soviet fisheries for Kamchatka River sockeye salmon are conducted by means of trap nets in Kamchatka Bay and drift nets in the Kamchatka River. From 1965 to 1980, 46.9% of the Soviet catch was taken in nets.

Although temperature (warm vs cold summers) did not influence the size of the catch in the river fishery, the Soviet catch is related to the relative abundance of group "*S*" fish. When the proportion of group "*S*" sockeye in the total escapement was high (i.e., if it exceeded 26% of the total spawning escapement), the total Soviet catch has been low.

The Kamchatka River sockeye salmon run occurs from early June to late July with about 80% of the total being taken in June. The specialized sockeye net fishery does not operate throughout June because chinook salmon (*Oncorhynchus tshawytscha*) are also subject to capture during part of that month. Until 1981, the pattern of fishing was usually as follows: At the beginning of the chinook run, large-meshed nets were used and these only took sockeye salmon incidentally. At the peak of the sockeye run (usually June 10–15), most fishermen switched to smaller-mesh nets and sockeye salmon then became the principal species in the catch. On some peak days of fishing, 50–60% of the daily sockeye run was caught; net fisheries were then curtailed, usually from June 21–30, to avoid overfishing. This pattern has been typical of fisheries in June since the 1930's or 1940's. Since 1981, however, net fisheries have been managed to take the relative abundance of groups "*S*" and "*E*" into account.

The production of group "*S*" is much lower than that of group "*E*"; the Bezymyanny volcano did not have a measurable affect on group "*E*" recruitment and the spawning escapements of group "*E*" have been inadequate during 1957–84. Group "*S*" sockeye are not predominant at the peak of the sockeye run but they enter the river over a long period. Consequently, group "*S*" sockeye do not attract heavy fishing effort, particularly when chinook salmon are abundant. It is more important to ensure an optimum escapement for group "*E*" than for group "*S*" for the following reasons: Fishing pressure can be diverted from group "*E*" by relocating trap nets in Kamchatka Bay and changing net fishing times in the river. A suitable regulation of the net fishery has already occurred, but special investigations will be required to determine how best to regulate trap net catches of group "*S*" sockeye. Although it is probably less costly to fish in the Kamchatka River in the traditional way with nets than to use other fishing methods, research has already shown that these methods are unacceptable.

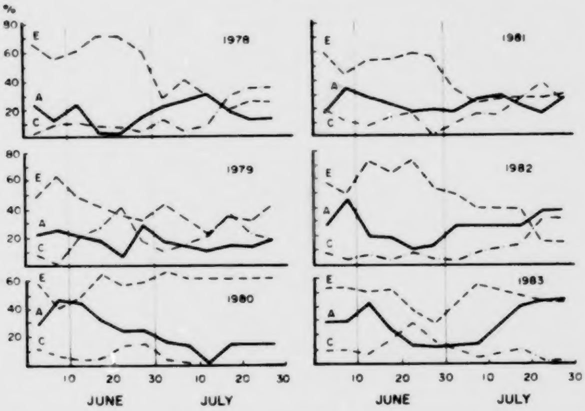

FIG. 10. Estimated percentage of Kamchatka River drift net catches of sockeye salmon contributed by groups "*E*" and "*S*" and stock "*A*" in June and July 1978–83.

About 70% of the total drift net catch of sockeye of stock "*A*" and groups "*E*" and "*S*" is taken in the period June 10–30 (Fig. 10), so net catches must be regulated during this period. Figure 10 also shows that the proportion of stock "*A*" sockeye was somewhat higher in the early part of the run (June 1–10) than during the peak (June 10–30). In view of the somewhat lower abundance of sockeye and the abundance of chinook salmon prior to June 10, it is unreasonable to target on sockeye before June 10–30. Although the proportion of stock "*A*" has usually declined during June 10–30, these fish could be harvested near the lake outlet since Azabachye Lake is near the river fishing area. Thus, the main concern is how to selectively harvest groups "*E*" and "*S*".

Group "*S*" fish made up a relatively high proportion of the June 15–25 catch in both 1979 and 1983 and increased in abundance relative to other stocks during that period, or a bit later in some years. Furthermore, in years when group "*S*" fish were relatively more numerous, group "*E*" fish were significantly less abundant. Under these circumstances, fishing pressure can be shifted from group "*E*" to group "*S*" by starting the specialized net fishery not at the beginning of the heavy run, but approximately 2–4 days later. In this way, and by keeping escapements relatively constant, an overall increase in the production of Kamchatka River sockeye salmon can be achieved without adversely affecting the total escapement.

Recommendations

The following recommendations will provide a rational basis for the management of Soviet fisheries on Kamchatka River sockeye stocks at their present level of abundance, given the continued existence of a Japanese high seas fishery:

1) It is necessary to increase spawning escapements, especially for group "*E*", to restore total stock abundance to a level at which the current annual catch of about 1.5–2.5 thousand t can be sustained.

2) Heavy net fishing is recommended to harvest successfully surplus production of group "*S*" sockeye during their peak occurrence in the catch.

3) Procedures should be established for fertilizing Azabachye Lake. If an increase in production of stock "*A*" results, a special fishery at the lake's outlet to the Kamchatka River should be created to harvest the surplus without affecting the escapement of other stocks.

4) Once optimum escapements of group "*E*" and group "*S*" have been achieved in cold years, harvesting decisions should be guided by the temperature conditions during incubation that influence both optimum escapement and spawning success.

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Rational Fishing of Sockeye Salmon (*Oncorhynchus nerka*) From the Ozernaya and Kamchatka Rivers

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Abstract

SELIFONOV, M. M. 1987. Rational fishing of sockeye salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka rivers, p. 403–407. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Fluctuations in abundance of Ozernaya sockeye salmon (*Oncorhynchus nerka*) are analyzed in relation to changes in fishing intensity. Yield in excess of 75% of the mature population results in a considerable decline in production. An incidental catch of immature fish in numbers exceeding the rate of natural mortality also reduces harvest potential. Effects of high seas fishing on the Ozernaya sockeye salmon population were examined. The high seas fishery is considered to be irrational, and should be reduced to a level which ensures an annual escapement of 1.6–2.3 million spawners. This should ensure strong production and consistently high catches.

Résumé

SELIFONOV, M. M. 1987. Rational fishing of sockeye salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka rivers, p. 403–407. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les fluctuations de l'abondance du saumon nerka (*Oncorhynchus nerka*) de l'Ozernaya sont analysées à la lumière des variations de la pression par pêche. Des rendements supérieurs à 75 % de la population mature entraînent un déclin marqué de la production. Des prises accessoires de poissons immatures en nombre supérieur au taux de mortalité naturelle mènent aussi à une baisse du potentiel d'exploitation. On examine les incidences de la pêche hauturière sur la population de saumon nerka de l'Ozernaya. On considère que la pêche hauturière est irrationnelle; elle devrait être réduite à une niveau assurant une échappée annuelle de 1,6 à 2,3 millions de géniteurs. On assurerait ainsi une forte production et des captures uniformément élevées.

In recent times, Far-eastern sockeye salmon (*Oncorhynchus nerka*) have been quite numerous but landings have been less than those of pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) (Levanidov et al. 1970). Asian sockeye salmon come primarily from two large rivers — the Ozernaya and Kamchatka rivers; during 1931–41, sockeye from these two rivers comprised nearly 87% of the total sockeye catch (Taguchi 1956) and currently, they constitute an average of 92% of the coastal sockeye catch.

The Ozernaya sockeye salmon stock fluctuates considerably in response to both environmental factors and the fishery. However, an intensive high seas fishery is the main factor determining abundance (Selifonov 1978). The purpose of this work is to assess the influence of fisheries on the abundance of the Ozernaya sockeye and to make recommendations for improving management of this resource.

Methods

Fish data were collected in the Ozernaya River estuary and at an observation site in the Kurile Lake area used by the Kamchatka branch of TINRO. Catch statistics from Soviet coastal fisheries and from the Soviet–Japanese Fisheries Commission for the years 1952–83 were also used in this analysis.

Offshore fishing methods for Ozernaya sockeye salmon for 1952–75 were described by Selifonov (1975). The relative abundance of both mature and immature age-groups in the catch differed between the periods 1972–75 and 1976–83. Stock-recruitment curves fitted by the least squares method (Ricker 1954) have been used to estimate optimum spawning escapements.

The abundance of Ozernaya sockeye was indexed in three ways: by spawning escapement, by the size of the Soviet coastal catch, and by the size of the Japanese high seas catches. These data are available since 1940, and provide a basis for dividing catch records into four "eras" according to the intensity of fishing: (1) intensive coastal fisheries, 1940–45; (2) coastal fisheries only, 1946–52; (3) intensive high seas fisheries, 1953–76; and (4) regulated high seas fisheries, 1977–present. The Ozernaya sockeye run has changed distinctively in each of these periods.

Results

The trend in abundance of Ozernaya sockeye salmon is summarized in 5-yr periods in Table 1. In the first period (1940–45), the coastal and high seas fisheries (combined) caught an average of 70% of the mature population and spawning escapements averaged 1.65 million fish annually. Reduced fishing effort from 1946 to 1950 resulted in lower rates of exploitation and allowed much larger escapements of spawners. Spawning escapements declined steadily in the third period (1952–76) and total abundance decreased to a minimum in the mid-1970's. When fishing was further reduced after 1977, both spawning escapement and total population size increased.

The general feature of these statistics is that the higher the exploitation rate, the lower the abundance of spawners and subsequent returns. Since the Soviet commercial catch was high only when the Japanese fisheries were not operating (1945–52), it appears that the unregulated high seas fishery has had the greatest impact on Ozernaya sockeye salmon stocks. However, the precise effects have yet to be assessed.

High seas fishing of salmon in the northwest Pacific began in 1952 and sockeye salmon catches reached a maximum in 1955–58. Japanese vessels caught 10–20 million fish annually in that period. Thereafter, catches dropped both in weight and number and by 1983, less than 2.5 million fish were caught annually (Table 2). A major reduction in catch occurred in 1971, followed by gradual reductions in subsequent years. This was a period of general decline for Asian sockeye salmon stocks. The decline in the mothership catch was offset to some extent by the increased drift-net catches by medium-sized vessels south of 40° N where many immature sockeye salmon were caught. This is confirmed by the fact that both the average weight of captured sockeye and the catch per unit of fishing effort dropped in the early stages of fishing (Table 3).

High seas fishing effort remained high in the 1953–76 period (Table 1) and the abundance of Ozernaya sockeye salmon fluctuated in synchrony with the total abundance of

TABLE 1. Fluctuations in abundance of Ozernaya River sockeye salmon (5-yr means).

Indices	Years								
	1940–1945	1946–1950	1951–1955	1956–1960	1961–1965	1966–1970	1971–1975	1976–1980	1981–1984
No. of mature fish (thousand)	5 525	4 608	6 104	7 046	5 187	3 914	1 975	2 172	3 275
Exploitation rate by high seas Japanese fishery, (%)	49.5	—	37.0	76.6	59.2	76.5	65.6	39.0	29.1
Exploitation rate by Soviet coastal fishery, (%)	20.7	53.1	41.0	12.8	21.1	7.7	11.6	10.8	19.7
Spawning escapement (thousands)	1 648	2 162	1 354	1 350	1 020	620	450	1 090	1 600
Total returns[a] (thousands)	4 762	6 080	6 949	4 781	3 532	1 919	2 239	—	—

[a] From spawning escapements in this time period.

TABLE 2. Japanese sockeye salmon catch by year in the northwest Pacific Ocean 1952–83.

	Catch (thousands)		
Year[a]	Motherships	Driftnets[b]	Total
1952	736	—	736
1953	1 547	—	1 547
1954	3 391	—	3 391
1955	11 057	—	11 057
1956	9 069	—	9 069
1957	19 399	—	19 399
1958	10 710	—	10 710
1959	9 125	—	9 125
1960	12 879	—	12 879
1961	12 998	—	12 998
1962	10 590	—	10 590
1963	8 902	—	8 902
1964	7 097	—	7 097
1965	12 038	—	12 038
1966	7 254	—	7 254
1967	8 087	2 492	10 579
1968	6 373	2 788	9 161
1969	5 935	2 467	8 402
1970	6 944	2 929	9 873
1971	3 554	2 996	6 550
1972	3 184	3 711	6 895
1973	2 613	3 308	5 921
1974	2 282	3 155	5 437
1975	2 171	2 969	5 140
1976	2 277	3 504	5 781
1977	1 508	1 289	2 797
1978	1 882	1 293	3 175
1979	2 186	757	2 943
1980	2 412	787	3 199
1981	2 224	859	3 083
1982	1 738	723	2 461
1983	1 655	828	2 483

[a] 1952–79 — data of INPFC |International North Pacific Fisheries Commission|, 1980–83 — Japanese annual catch statistics.

[b] *Ed. Note:* These data pertain to the Japanese landbased offshore driftnet fishery. The mothership fishery catcher boats also fish with driftnets.

TABLE 3. Average annual weight, and catch per unit of fishing effort for sockeye salmon in the high seas fishery, 1962–83[a].

Year	Weight (kg)			Catch per fishing effort, *p*		
	Mother-ships	Drift-nets[b]	Average	Mother-ships	Drift-nets	Average
1962	2.32	—	2.32	1.81	—	1.81
1963	2.14	—	2.14	1.50	—	1.50
1964	1.99	—	1.99	0.94	—	0.94
1965	2.05	—	2.05	1.97	—	1.97
1966	2.16	—	2.16	1.40	—	1.40
1967	2.06	1.48	1.93	1.55	0.42	0.95
1968	2.01	1.43	1.83	1.08	0.45	0.75
1969	1.97	1.55	1.84	0.96	0.39	0.67
1970	1.87	1.65	1.81	1.15	0.49	0.82
1971	1.81	1.52	1.68	0.61	0.63	0.62
1972	1.69	1.51	1.60	0.54	0.72	0.62
1973	1.80	1.42	1.58	0.45	0.57	0.51
1974	1.72	1.34	1.50	0.42	0.52	0.47
1975	1.71	1.35	1.50	0.39	0.50	0.44
1976	1.73	1.39	1.52	0.39	0.59	0.49
1977	1.76	1.39	1.59	0.38	0.35	0.36
1978	1.78	1.40	1.62	0.69	0.38	0.52
1979	1.80	1.38	1.69	0.78	0.24	0.49
1980	1.91	1.41	1.78	0.77	0.25	0.51
1981	1.71	1.50	1.65	0.76	0.26	0.50
1982	1.75	1.51	1.68	0.59	0.24	0.42
1983	1.81	1.66	1.76	0.56	0.27	0.41

[a] Estimates on the basis of statistics provided annually by Japan.

[b] *Ed. Note:* See footnote b, Table 2.

Asian sockeye salmon. The abundance of mature fish was estimated at 6 million prior to high seas fishing (Egorova 1964). It is also estimated that Ozernaya sockeye accounted for half the total high seas catch of sockeye in some years but that this proportion declined to 17–22% in the early 1970's, concurrent with the decline in total catch. In recent years, about 30% of Ozernaya sockeye salmon were taken in the offshore fisheries.

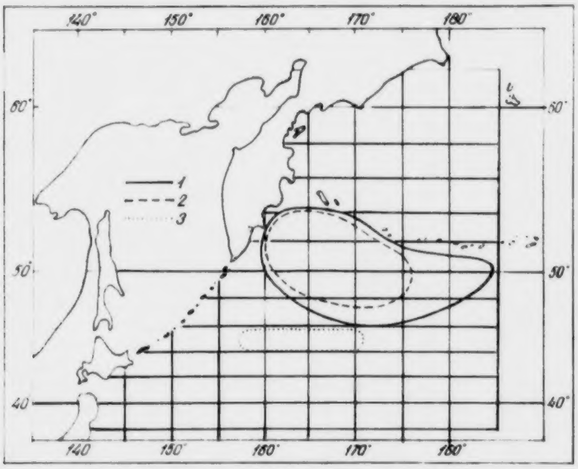

FIG. 1. The main areas of catch of Ozernaya sockeye salmon in the northwest Pacific: 1. May–June, 2. July, 3. immatures.

The long-term trends in catches of Ozernaya sockeye salmon in the northwest Pacific are consistent with the following life history suggested by Konovalov (1971). In spring, both mature and immature fish are concentrated to the south of the Aleutian ridge, but mature fish occupy a larger area, since some early-spawning fish will have begun their return migration (Fig. 1). Kamchatka sockeye stocks are also found throughout this area and some American sockeye are found in the eastern part of the area.

In the first half of the fishing season beginning in late May, sockeye salmon from the Kamchatka River are predominant in the offshore catches. These sockeye begin their spawning migration and mature earlier than Ozernaya sockeye salmon (Birman 1958; Konovalov 1971; Hanamura 1966). By late June, catches in the area of 46–54° N and 160°–175° E are almost entirely of Ozernaya sockeye (Selifonov 1975). Many mature fish are caught in the centre of this area, mainly in June. The incidental catch of immature fish is small in this period whereas it accounts for most of the catch in July.

An effective drift-net fishery has been developing south of 48° N since 1967, but an incidental catch of immature fish has also occurred, reaching a maximum of about 75% of the catch in 1972. The catch of immature Ozernaya sockeye salmon fluctuated between 12.2 and 19.6% (average 15.5%) in all zones where Japanese vessels fished from 1962 to 1966, and between 16.5 and 64.0% (average 37.4%) for all sockeye populations combined (Selifonov 1982).

A protracted period of very heavy exploitation adversely affected the Ozernaya sockeye salmon stock. Removal of a great number of mature fish resulted in very low spawning escapements and a further decline in stock abundance. The situation was exacerbated by the large catch of immature fish by the high seas drift-net fishery. This was not very apparent while the incidental catch rate was below or close to the rate of natural mortality. However, as the catch of immature salmon increased, recruitment of mature fish declined considerably.

TABLE 4. Loss of biomass due to catch of immature Ozernaya sockeye salmon on the high seas (estimates from numbers of fish).

Year	Catch (tonnes)			Loss			
	High seas	Possible on the coast		(tonnes)		(%)	
		R_x[a]	P_x	R_x	P_x	R_x	P_x
1962	934	1 405	1 589	471	655	33.5	41.2
1963	921	1 508	1 706	587	785	38.9	46.0
1964	353	579	650	226	297	39.0	45.7
1965	618	924	1 044	306	426	33.1	40.8
1966	519	842	956	323	437	38.4	45.7
1967	2 240	3 834	4 331	1 594	2 091	41.6	48.3
1968	1 918	2 801	3 163	883	1 245	31.5	39.4
1969	622	1 049	1 189	427	567	40.7	47.7
1970	2 110	3 274	3 563	1 164	1 453	35.6	40.8
1971	971	1 707	1 926	736	955	43.1	49.6
1972	1 673	3 058	3 458	1 385	1 785	45.3	51.6
Average	1 171	1 907	2 143	736	972	38.6	45.4

[a] R_x and P_x are calculated using coefficients of instantaneous mortality of Ricker (1962) and Parker (1962), respectively.

The high seas catch has been reduced to 30–40% of the total catch since 1977 and the total exploitation rate by all fisheries no longer exceeds 50%. Since then, both the total number of spawners and the average stock abundance have increased.

An unfavourable aspect of the high seas sockeye salmon fishery is that fish are caught before they have reached their maximum size at maturity. The loss in potential biomass which occurs when fish are caught one year prior to maturity exceeds the natural loss through mortality (Selifonov 1978). The example calculated in Table 4 demonstrates the irrationality of fishing sockeye salmon on the high seas. Losses are estimated for immature sockeye salmon caught in their second year of sea life, one year before maturity. The coefficients of natural mortality are those of Ricker (1962), i.e., 0.0382 per month (or 24.10% during the second year), and Parker (1962), i.e., 0.0267 a month (or 14.24% during the second year). It is quite obvious that such annual losses of biomass fluctuate considerably, but they can reach quite a large value (736–972 tonnes) and equivalent to 38.6–45.5% of the catch. Thus, about one thousand tonnes of production are lost annually as a result of the offshore catch of immature sockeye salmon.

Heavy exploitation of mature and immature fish influences population structure (Selifonov 1982). In the 1971–75 period of decline, the average age of Ozernaya sockeye decreased and consequently the reproductive potential of escapements declined.

Discussion

The irrationality of the high seas sockeye fishery in the northwest Pacific may be summarized as follows:

1) An exploitation rate in excess of 75% of the mature stock, including a high seas catch of 59.2–76.7% has resulted in reduced escapements, a younger average age at maturity and reduced reproductive capacity. Subsequently, these changes caused a drastic decline in total abundance.

2) The incidental catch of large numbers of immature fish (as high as 64% of the total catch in some years) reduced recruitment of mature fish available to the fishery in the following years.

3) The removal of both mature and immature sockeye on the high seas represents a direct loss of potential biomass since the rate of increase in population biomass due to growth considerably exceeds losses due to natural mortality at this stage of maturity. In addition, this premature exploitation generally precludes the opportunity to harvest valuable byproducts such as caviar.

4) Exploitation of mixed stocks will inevitably result in overexploitation of unproductive stocks or underexploitation of more productive stocks.

5) When sockeye salmon and other salmonids are caught by high seas drift nets, large "indirect" losses occur. These losses can fluctuate widely and may exceed 50% of the total catch (Andreev and Sinelnikov 1982).

These facts show that the fishery is a powerful regulator of population abundance. Ultimately population strength depends upon the size of the escapement. Thus, in determining a rational strategy for exploiting Ozernaya sockeye, it is essential to estimate the optimum numbers of spawners. Ricker stock-recruitment curves were therefore fitted by the least squares method (Ricker 1954) to data from periods of both high abundance of parents and progeny (brood-years 1940–56) and low abundance (brood years 1957–69). For the period of high abundance, the equation was:

$$R_1 = 9.583S\, e^{-0.443S}$$

Thus a peak escapement of 2.26 million produced a return of 7.98 million. For the low abundance period the equation was:

$$R_2 = 7.452S\, e^{-0.607S}$$

In this period, a peak escapement of 1.65 million gave a return of 4.53 million. Thus, an average maximum yield of 64–72% of the mature stock should be possible given optimum escapements if this model is correct.

Recommendations for Management

We think a rational strategy for managing Ozernaya sockeye salmon must consist of the following:

1) An annual escapement of 1.6–2.3 million spawners to ensure successful reproduction and maximum yield.

2) Termination of the largely unfavorable high seas fishery in the northwest Pacific. The high seas fishery has been regulated since 1977, and the annual catch quota has been set at 42.5 thousand tonnes, including not more than 23.5 thousand tonnes inside the Soviet 200 mile zone. The total catch of sockeye salmon is not to exceed 1.1 million fish ±10%. In addition, both closed areas and areas where ony limited fishing is permitted have been established. These measures have helped to preserve sockeye stocks but are still insufficient. The incidental catch of immature sockeye remains excessive and should be reduced until fishing mortality on these fish is less than half the natural mortality rate; this corresponds to an incidental catch of about 10% of the biomass of Ozernaya sockeye.

3) A review of the desirability of coastal fisheries as an alternative to high seas fishing.

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Differentiation of Subpopulations of Sockeye Salmon (*Oncorhynchus nerka*), Karluk River System, Alaska

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Abstract

GARD, R., B. DRUCKER, AND R. FAGEN. 1987. Differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*), Karluk River System , Alaska, p. 408-418. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

We found that the sockeye salmon (*Oncorhynchus nerka*) run in the Karluk River system, Alaska, was differentiated into temporal or spatial subpopulations on the basis of biological and anatomical characteristics. Statistically significant ($P<0.05$) differences in freshwater and ocean age, length, and fecundity of spawners, and in length of fry were demonstrated between seasons or between spawning areas. Discriminant analysis using freshwater age, length, girth, fecundity, and egg volume showed good temporal (90% nonoverlap) and moderate spatial (25% nonoverlap) separation of spawners from different seasons or spawning grounds. Since it is probable that at least part of each character or character group difference is due to heredity, we expect that further studies will find one or more distinct subpopulations using each principal spawning ground.

Résumé

GARD, R., B. DRUCKER, AND R. FAGEN. 1987. Differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*), Karluk River System, Alaska, p. 408–418. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Selon les auteurs, la remonte de saumons nerkas (*Oncorhynchus nerka*) dans le système de la rivière Karluk (Alaska) est composée de sous-populations pouvant être différenciées sur les plans temporel et spatial d'après des caractéristiques biologiques et anatomiques. Ils ont observé des différences statistiquement significatives ($P<0.05$) entre les saisons et entre les frayères pour ce qui est de l'âge en eau douce et en eau salée, de la longueur et de la fécondité des reproducteurs et de la longueur des alevins. Une analyse discriminante portant sur l'âge en eau douce, la longueur, la circonférence du corps, la fécondité et le volume d'oeufs a révélé une bonne différenciation temporelle (90 % de non-chevauchement) et une différenciation spatiale modérée (25 % de non-chevauchement) des reproducteurs capturés à différentes saisons ou dans différentes frayères. Étant donné qu'au moins une partie de la différence entre chaque caractère ou groupe de caractères est due probablement à l'hérédité, il faut s'attendre à ce que des études ultérieures révèlent la présence d'une ou plusieurs sous-populations distinctes utilisant chaque frayère principale.

At one time the Karluk River system on Kodiak Island, Alaska (Fig. 1), was for its size one of the greatest sockeye salmon (*Oncorhynchus nerka*) producers in the world. Commercial fishing on Karluk sockeye salmon began in 1882 and developed rapidly; between 1888 and 1907, estimated annual catches of 2–3 million fish and runs of 4–5 million fish were common (Rounsefell 1958). The runs declined irregularly after 1907 and have numbered between 0.2 and 1.6 million fish in recent years.

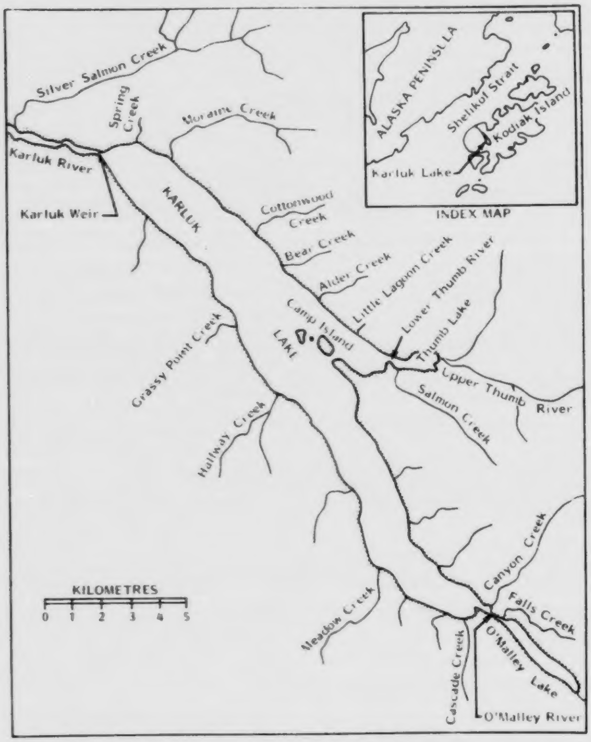

FIG. 1. Karluk River system, Kodiak Island, Alaska.

Many theories have been proposed to explain the long-term decline of the Karluk River sockeye salmon, including overfishing of productive midseason subpopulations[1] (Thompson 1950). This theory was based primarily on the long-term change from a unimodal to a bimodal seasonal distribution of the run. It was necessarily predicated on the existence of subpopulations which had not been substantiated in 1950.

Thompson's theory stimulated research and debate. Rounsefell (1958) concluded that the entire run of sockeye salmon to the Karluk River system belonged to a single population and hence rejected Thompson's theory. While not concerning themselves specifically with the subpopulation question, Owen et al. (1962) suggested that differential fishing on unequally productive segments of the Karluk run could have been responsible for the decline. Hartman and Raleigh (1964) identified an isolating mechanism which would permit subpopulations to develop when they discovered that most Karluk sockeye homed to specific tributaries. Further, Raleigh (1967) verified the existence of at least two subpopulations of sockeye, whose fry migrated to Karluk Lake by swimming in opposite directions relative to the current. Most recently, Wilmot and Burger (1985) proved that spring- and fall-run Karluk sockeye were distinct subpopulations as determined by electrophoretic studies of enzymes. The purpose of the present study is to present additional evidence for the existence of subpopulations of Karluk sockeye salmon which differ by timing and place of spawning; by age, length, girth, fecundity, and egg volume of spawners; or by timing and length of migrating fry. Observations made between 1962 and 1965 are reported.

Description of the Karluk River System

The Karluk River system is composed of Karluk Lake, Karluk River, and several tributary streams, two of which are connected to Thumb (106 ha) and O'Malley (215 ha) lakes. Karluk Lake is located at an elevation of 107 m near the northwest end of Kodiak Island (Fig. 1). It is 19 km long and 3 km wide with a surface area of 3 950 ha, and has a maximum depth of 126 m (Gilbert and Rich 1927). Karluk River flows north from the lake about 37 km to Shelikof Strait. The climate is cool and wet in summer and cold and snowy in winter, when the lake is often covered by ice.

Four distinct spawning habitats are used by sockeye salmon in the Karluk system: (1) lateral streams (e.g., Grassy Point, Cottonwood, and Meadow creeks); (2) terminal streams (Canyon Creek and Thumb and O'Malley rivers); (3) lake beaches, e.g., near the mouths of Thumb and O'Malley rivers; and (4) the upper part of Karluk River (Fig. 1). Lateral streams are generally short, steep, narrow, and shallow and have thin rubble substrates; terminal streams and Karluk River are long, of low gradient, wide, and deep and have thick gravel substrates. Karluk River differs from the terminal streams mainly in its greater volume flow. Beach spawning areas have gravel substrates and are generally in deeper, slower moving water than are stream or river spawning grounds.

Methods

TIMING AND DISTRIBUTION OF SPAWNING

To determine number of fish in the escapements to the system and individual streams and time of spawning at various locations, we counted adults at weirs and on foot surveys. For all 4 yr of the study, a picket weir was installed each May in Karluk River about 300 m downstream from the lake outlet, and adult salmon were counted daily until near the end of the run (late September to late October). For the years 1962–64, spawning salmon in important tributaries were counted weekly or biweekly (1964 only) using foot surveys. The estimated number of spawning salmon was the average of independent counts by two observers.

BIOLOGICAL CHARACTERISTICS OF SPAWNERS

Samples for determining age, length, and fecundity of female spawners were taken from Karluk weir, from weirs on Grassy Point, Meadow, and Canyon creeks, and from the spawning grounds.

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[1] Thompson assumed that the run was composed of self-sustaining units whose differences were heritable. Such units were called "subpopulations" by Marr (1957) and that term is used in this report.

At Karluk weir, every fourth day a random sample of 40 to 80 adults (1962) or 0.5% of the escapement for the preceding 4 days (1963-65) was assessed for mideye-fork length and sex, and scales were taken for age analysis. In the fall of 1965, otoliths were collected for age analysis because erosion of the 1963 and 1964 fall scale margins prevented accurate determination of ocean age. Between 1963 and 1965, all eggs were removed from 10% of the females sampled and were preserved in 10% formalin. All eggs from each female were counted manually.

Weirs were installed near the mouths of Grassy Point, Meadow, and Canyon creeks in the spring of 1962, 1963, and 1965. Random samples of about 30 females were collected at all the weirs in July and at Canyon Creek weir again in September (except 1965). An additional 100 to 200 females were measured at each site. In 1963 the study was broadened to include samples from Thumb Beach, Cottonwood Creek, Upper Thumb, Lower Thumb, and O'Malley rivers. These samples were obtained with a beach seine. The sampling program of 1963 was repeated in 1965 except that otoliths were collected to determine age, and maximum girth and egg volume were determined to increase the information relating to fecundity. Maximum girth was measured with a flexible tape and egg volume was measured by the displacement method.

TIMING, MIGRATION PATTERN, AND LENGTH OF MIGRATING FRY

To determine timing, migration pattern, and length of fry descending into Karluk Lake, we set two traps across the mouth of Grassy Point Creek and three traps across the mouth of Canyon Creek in 1963 and 1964. The traps were installed in early April and fished nightly until catches of fry became negligible. Numbers of fry caught in all traps were recorded each night. Fork lengths of about 40 fry from each creek were determined weekly during the migration period.

DATA ANALYSIS PROCEDURES

Functional linear regression coefficients were computed for fecundity-length data for each spawning ground and weir sample using methods outlined in Ricker (1973). Possible differences in slopes of regression lines of lateral and terminal stream samples and spring and fall samples were determined using an appropriate form of the *t* test (Clarke 1980: 442-443). Samples used to test for difference between lateral and terminal streams consisted of the total number of observations for terminal streams and every second observation for lateral streams. Samples used to test for difference between spring and fall seasons consisted of every second observation for spring spawning grounds and every third observation for fall spawning grounds and Karluk weir. Random subsampling of the data was necessary to reduce the number of observations for each sample below 200, which was the maximum number allowed by the then-current version of the Minitab statistical program used.

Linear discriminant function analysis of lateral spring, terminal spring, and terminal fall spawning groups, and convex polygon (convex hull) plots of the three groups, were done using the S data analysis and graphics system (Becker and Chambers 1984) on a Digital Equipment Corporation VAX 11/780. Characters used in the analysis were length (mm), egg number, girth (mm), egg volume (cc), and freshwater age (yr).

Results

TIMING AND DISTRIBUTION OF SPAWNING

The following results are based on spawning ground observations in 1963, when spawning began about July 1 and lasted until about November 1 (Fig. 2). The peak escapements into Karluk Lake through the weir were on June 15 and August 24. Following the pattern of their arrival at the lake, fish appeared on the spawning tributaries in two well-separated waves, which are called the spring and fall runs. The peak of the spring run was about July 19 and of the fall run about September 14. A midseason low occurred August 15. Assuming that the peak escapements at the weir and in the tributaries were composed of the same fish, the migration between the weir and the spawning grounds took about 5 wk for the spring run and 3 wk for the fall run. Spring run fish probably stayed longer in the lake than fall run fish because upon arrival at the lake they were not as sexually mature and required more time to ripen. Secondary sexual characteristics — red coloration in both sexes and elongation of the lower jaw in males — of fish passing through Karluk weir were not as far advanced in the spring as they were in the fall.

Some segregation of spawners by type of spawning habitat by season was evident in 1963 (Fig. 2). Lateral stream spawners were 91% from the spring run while terminal stream spawners were from both the spring and fall runs: Upper Thumb River was occupied mainly by the spring run, Canyon Creek and O'Malley River by both runs, and Lower Thumb River by the fall run. Most of the spring run fish in Lower Thumb River were enroute to Salmon Creek and Upper Thumb River. Upper Karluk River and most of the lake beaches were used exclusively by fall run fish. Gard and Drucker (1965) estimated that 10% of the escapement spawned in upper Karluk River below the weir in 1963; no attempt was made to census beach spawners.

The temporal and spatial pattern of spawning recorded in detail in 1963 was similar to that of 1962 and 1964 (our data) and 1957, 1958, and 1959 (Owen et al. 1962). After reading the diaries of Willis H. Rich (1963), Owen et al. concluded that as early as 1922 the timing and distribution of spawners were basically similar to the present except that the more numerous earlier spawners extended to higher elevations in the tributaries and over longer periods of time.

AGE

Most Karluk sockeye salmon spend from 1 to 5 yr in fresh water and from 0 to 3 yr in the ocean before returning to their natal stream or lake gravels to spawn and die. Twenty-two different combinations of freshwater and ocean ages have been recorded for Karluk fish, but the most common are 5_3, 6_4, 6_3, and 7_4 types.[2].

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[2] A 5_3 fish is one that lived in fresh water for 3 yr (including 10 months in the gravel), in salt water for 2 yr, and spawned and died at 5 yr of age.

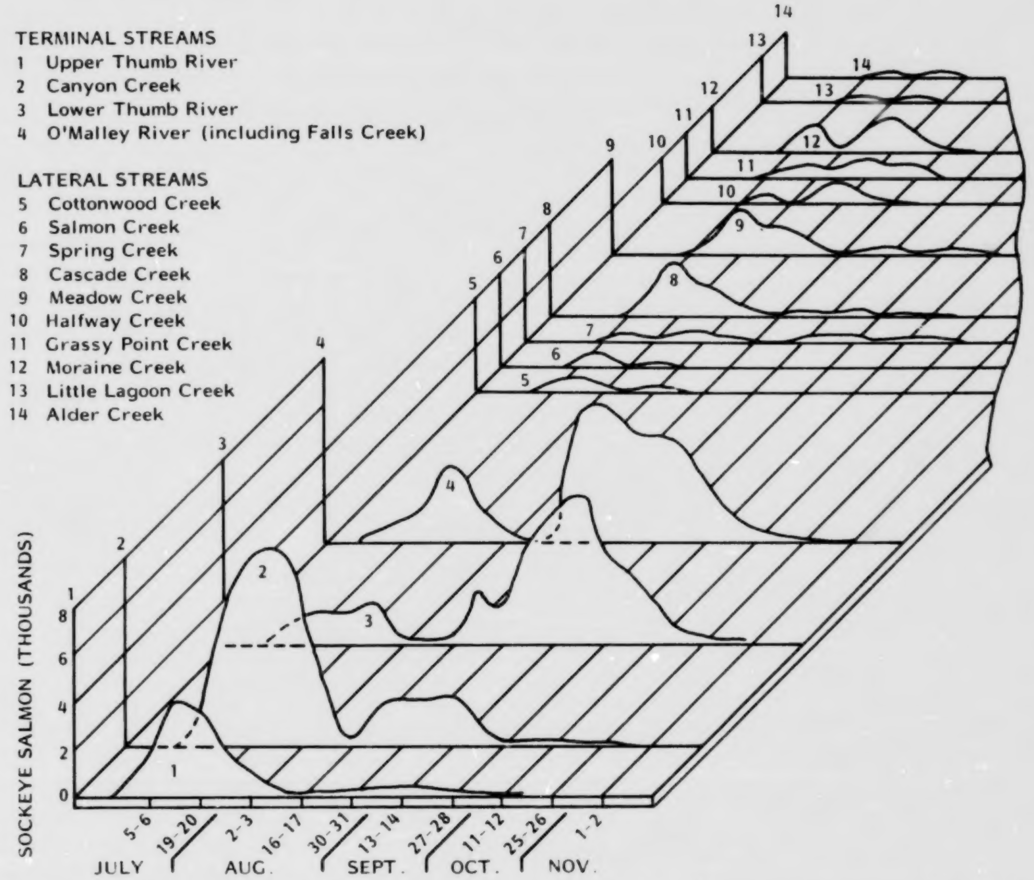

FIG. 2. Timing and distribution of sockeye salmon on spawning grounds by weekly stream survey counts, Karluk Lake, 1963.

TABLE 1. Number of female sockeye salmon in principal freshwater and ocean age groups from Karluk weir and spawning grounds, 1962, 1963, 1965. The percentages of total number of fish in the age-group are shown in parentheses.

Place and season of sampling	1962		1963		1965			
	Freshwater age (yr)		Freshwater age (yr)		Freshwater age (yr)		Ocean age (yr)	
	3	4	3	4	3	4	2	3
Karluk weir								
Spring	373(89)	45(11)	239(84)	45(16)	80(60)	53(40)	75(55)	61(45)
Fall	548(95)	31(5)	156(42)	212(58)	45(31)	100(69)	134(92)	11(8)
Spawning grounds								
Spring	31(61)	20(39)	85(79)	23(21)	73(49)	76(51)	146(99)	2(1)
Fall	22(100)	0(0)	34(56)	27(44)	7(8)	82(92)	85(96)	4(4)

The relative abundance of the principal freshwater age-groups varies seasonally, the usual pattern being a decrease in 3-yr fish and an increase in 4-yr fish between spring and fall (Barnaby 1944). In our studies, significant (X^2; $P<0.01$) seasonal changes in abundance of freshwater types occurred at Karluk weir and on the spawning grounds in 1963 and 1965, but not in 1962 (Table 1). The aberrant situation in 1962 probably resulted from the disparate fall escapements of 1956 and 1957, the brood years of 6_4 and 5_3 fish in the 1962 escapement. Only about half as many fish spawned in the fall of 1956 as in the fall of 1957. Hence spawners from these years contributed relatively few fish of age 6_4 and many of age 5_3 to the 1962 fall escapement.

We also tested for differences in proportions of freshwater ages 3 and 4 between spring run sockeye salmon from lateral and terminal streams, but no consistent differences were detected.

Our 1965 data permitted comparison of the relationship between freshwater and ocean ages at Karluk weir and on the spawning grounds. Barnaby (1944) presented data that

Rounsefell (1958) used to demonstrate that ocean age is negatively related to freshwater age. Since freshwater age increases with time during the adult run, it should follow that ocean age would decrease during the same period. In most years since 1922, both Barnaby (1944) and Rounsefell (1958) did indeed find an increase in 2-yr-ocean fish and a decrease in 3-yr-ocean fish between spring and fall runs. In 1965, we found a similar significant (X^2; $P<0.05$) shift in the 2- and 3-yr-ocean types at Karluk weir but not among fish of these same ages on the spawning grounds (Table 1). Most of the fish sampled on the spawning grounds were 2-yr-ocean types during both spring and fall runs. Perhaps the abundant 3-yr-ocean fish that passed through Karluk weir in the spring spawned mostly on lake beaches or in tributaries not sampled.

LENGTH

The lengths of female sockeye salmon from the weir and the spawning grounds for 1962, 1963, and 1965 were studied to determine if differences occurred between seasons or areas. Fall run females measured at Karluk weir in 1962 were significantly (t; $P<0.01$) longer than spring run females (Fig. 3). Among spawning ground salmon, fall run females were longer than spring run females in Canyon Creek (a terminal stream), which in turn were longer than spring run females in Meadow and Grassy Point creeks (lateral streams) (t; $P<0.01$). In an expanded series of samples collected in 1963 (Fig. 4), a similar pattern was evident except that females in Meadow Creek were somewhat longer than those in Canyon Creek. Spring-run females in Canyon Creek and

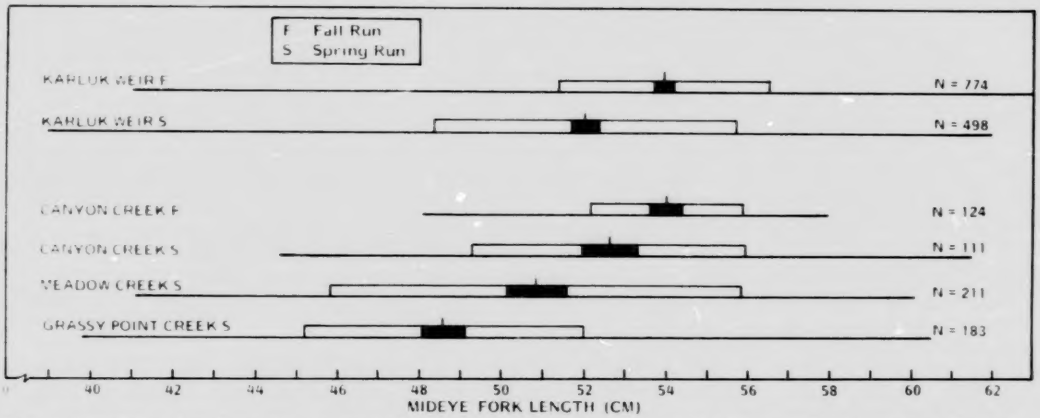

FIG. 3. Lengths of female sockeye salmon of mixes ages from Karluk weir and four spawning grounds in the Karluk system, 1962. Ranges are indicated by the horizontal lines, means by the vertical lines, two standard errors of the mean by the black bars on each side of the mean, and one standard deviation by the black bar plus the white bar on each side of the mean.

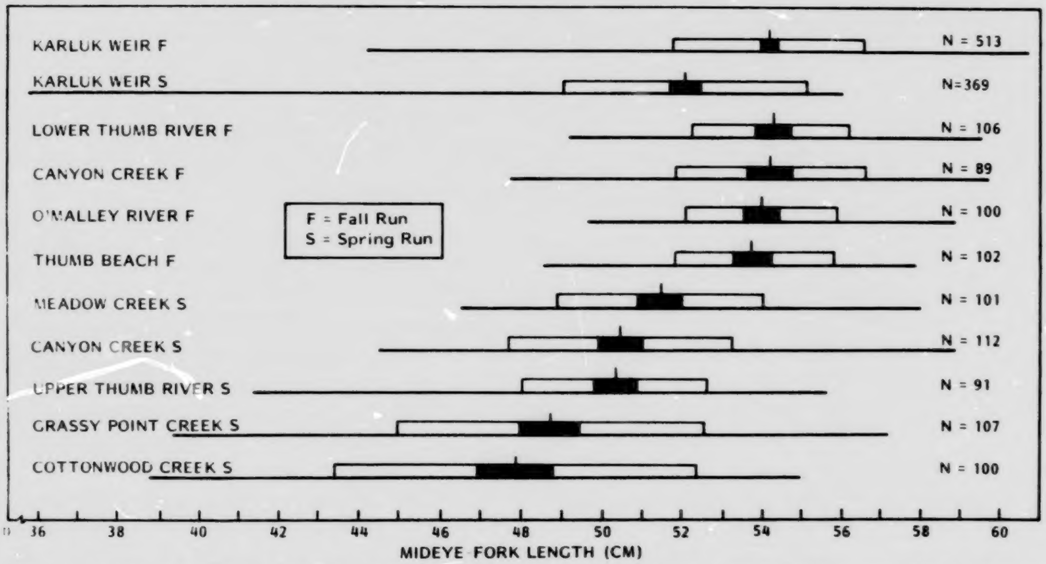

FIG. 4. Lengths of female sockeye salmon of mixed ages from Karluk weir and nine spawning grounds in the Karluk system, 1963. Ranges are indicated by the horizontal lines, means by the vertical lines, two standard errors of the mean by the black bars on each side of the mean, and one standard deviation by the black bar plus the white bar on each side of the mean.

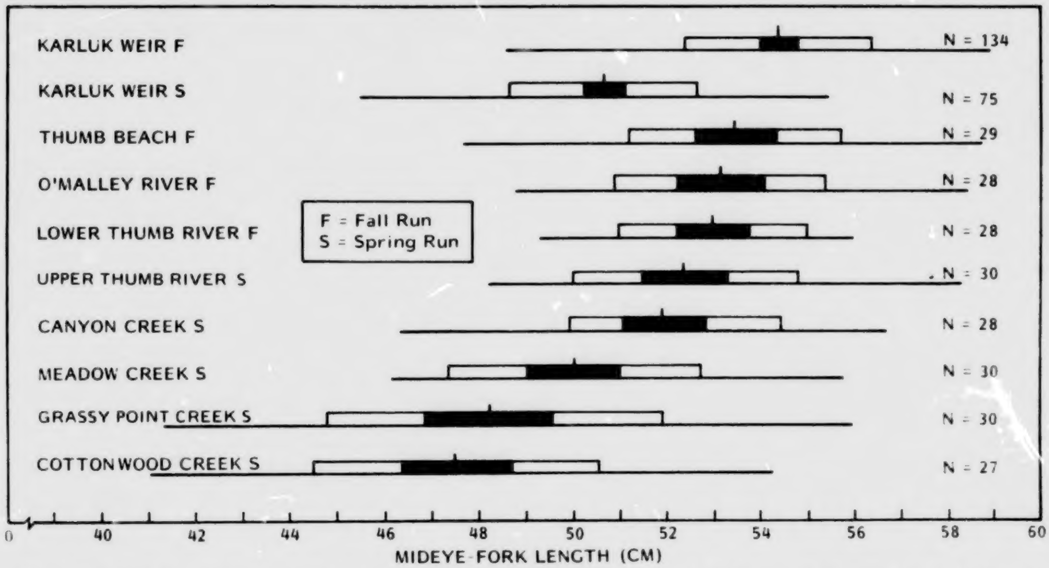

FIG. 5. Lengths of 2-yr-ocean female sockeye salmon from Karluk weir and eight spawning grounds in the Karluk system, 1965. Ranges are indicated by the horizontal lines, means by the vertical lines, two standard errors of the mean by the black bars on each side of the mean, and one standard deviation by the black bar plus the white bar on each side of the mean.

Upper Thumb River (terminal streams) were similar in length, as were females in Grassy Point and Cottonwood creeks (laterals streams). Vernon (1957) found that length of male and female kokanee (landlocked sockeye salmon) from separate arms of Kootenay Lake, British Columbia, were consistently different over a 4-yr period. No age determinations were made for fish measured in 1962 and 1963.

Ocean age has a profound influence on salmon lengths, and to determine the effect of ocean age on our observed 1962 and 1963 size differences, lengths of 2-yr-ocean females of the spring and fall runs were compared in 1965 (Fig. 5). The pattern of the earlier years prevailed, although the lengths of spring and fall run fish from terminal streams did not differ significantly (t; $P<0.05$). Sample size was reduced in 1965 to the minimum needed for a representative sample in view of the need to kill fish in order to age them from otoliths. Non-significant differences in length of spring and fall run fish from terminal streams were probably due to small sample sizes, rather than to presence of only 2-yr-ocean fish in the samples, because a clear-cut difference between lengths of fish from spring and fall runs occurred at Karluk weir where the samples were larger.

To sum up the foregoing paragraphs: (1) Fall run sockeye salmon were consistently longer than spring run sockeye salmon, and fish from terminal streams were generally longer than fish from lateral streams. (2) Seasonal and spatial differences in lengths of salmon in the Karluk system were not, for the most part, due to differences in ocean age.

FECUNDITY

The objective of our study of fecundity (number of mature eggs per spawning female) was to determine if there were differences between groups of salmon spawning at different seasons or places in the Karluk River system. Variation in the fecundity of sockeye salmon within a single-lake system such as Karluk has received little attention, although studies have shown that fecundity varies between river systems (Hartman and Conkle 1960; Foerster 1968; Ivankov and Andreyev 1969) and between lakes in the same river system (Aro and Broadhead 1950).

Since the number of eggs contained by any fish is closely related to its length, a mathematical expression relating these variables is necessary when fish of different lengths are compared. The relationship is curvilinear in salmonids that mature over a broad size range (Smith 1947; Vladykov 1956). However, since sockeye salmon mature over a narrow size range, a linear equation may adequately describe the relationship (Foerster and Pritchard 1941; Rounsefell 1957). To test for curvilinearity in the fecundity-length relationship for Karluk River sockeye salmon, we did a polynomial regression analysis using the 1965 spawning ground and spring weir samples and determined that addition of a quadratic term in length did not detectably improve the fit. Therefore, we used linear regression techniques in subsequent analyses.

Results of the analyses (Table 2) indicated that slopes of the regression lines for lateral and terminal streams were not significantly different (t; $P<0.05$), but that slopes of the regression lines for spring and fall runs were significantly (t; $P<0.01$) different (Table 3). That the fecundity-length relationship may be used in separating spring and fall subpopulations of sockeye salmon in the Karluk River system is evident from the functional regression lines graphed in Fig. 6, 7, and 8. With the exception of the 1965 spring sample from Canyon Creek, regression lines for fall samples were steeper than those for spring samples within each year.

DISCRIMINANT FUNCTION ANALYSIS

The first and second discriminant functions (correlations of 82% and 33%, respectively) differentiated three groups

TABLE 2. Mean mideye-fork length and fecundity of sockeye salmon from Karluk weir and the spawning grounds of Karluk Lake, 1962–65. Spring run fish were collected from June to mid-July and fall run fish from late July to October.

Year, sample site and lateral (ℓ) or terminal (t) location	Run sampled	Number of females	Mean mideye-fork length (cm)	Mean fecundity	Intercept (*a*)	Slope (*b*)
1962						
Grassy Point Creek (ℓ)	Spring	30	50.5	2 197	−3 879	120.3
Meadow Creek (ℓ)	Spring	29	53.2	2 708	−3 572	118.0
Canyon Creek (t)	Spring	28	53.1	2 802	−3 132	111.6
Canyon Creek (t)	Fall	30	54.0	3 641	−6 918	195.5
1963						
Karluk weir	Spring	44	52.4	2 834	−5 791	164.5
Karluk weir	Fall	58	54.3	3 435	−7 375	199.1
Grassy Point Creek (ℓ)	Spring	31	49.1	2 225	−4 390	134.7
Meadow Creek (ℓ)	Spring	30	51.1	2 289	−5 486	152.2
Cottonwood Creek (ℓ)	Spring	30	48.3	2 268	−3 612	121.8
Upper Thumb River (t)	Spring	30	50.1	2 658	−4 538	143.6
Canyon Creek (t)	Spring	36	52.1	2 728	−2 985	109.7
Canyon Creek (t)	Fall	19	55.1	3 638	−6 283	180.0
O'Malley River (t)	Fall	30	54.2	3 736	−8 886	232.9
Lower Thumb River (t)	Fall	32	54.7	3 719	−7 188	199.4
Thumb Beach (t)	Fall	32	53.5	3 514	−8 923	232.5
1965						
Karluk weir	Spring	14	51.5	2 811	−6 337	177.5
Karluk weir	Fall	144	54.5	3 618	−10 860	265.7
Grassy Point Creek (ℓ)	Spring	30	48.2	2 264	−4 633	143.1
Meadow Creek (ℓ)	Spring	30	50.1	2 605	−6 507	182.0
Cottonwood Creek (ℓ)	Spring	29	47.3	2 145	−4 703	144.8
Upper Thumb River (t)	Spring	29	52.3	2 895	−6 901	187.4
Canyon Creek (t)	Spring	30	52.0	2 935	−8 380	217.4
O'Malley River (t)	Fall	29	53.4	3 792	−8 556	231.2
Lower Thumb River (t)	Fall	30	53.3	3 705	−13 341	319.9
Thumb Beach (t)	Fall	30	53.6	3 576	−7 112	199.3

of fish: lateral stream spawners (all spring), terminal spring spawners, and terminal fall spawners. The first and third groups were clearly differentiated by the first discriminant function (10% overlap, Fig. 9) whereas the terminal spring spawners overlapped the other groups almost completely and were not differentiated either by the first or by the second discriminant function.

TIMING, BEHAVIOR, AND LENGTH OF MIGRATING FRY

Although the progeny of Karluk Lake spawners emerge directly into the lake, the fry whose genesis is either a tributary stream or upper Karluk River must migrate to reach

TABLE 3. Tests of slopes of functional regression lines involving fecundity and mideye-fork length of sockeye salmon in Karluk River.

Test	Sample	Sample size (n)	Correlation coefficient squared (r^2)	Slope of regression line (b)	T Value	Degrees of freedom
Lateral vs. terminal streams	Lateral-spring	119	0.585	13.20		
	Terminal-spring	153	0.371	14.42	1.01$^{n.s.}$	138
Spring vs. fall runs	Spring	196	0.581	14.78		
	Fall	175	0.407	23.22	6.09**	284

n.s. Not significant.
** Significant at $P<0.01$.

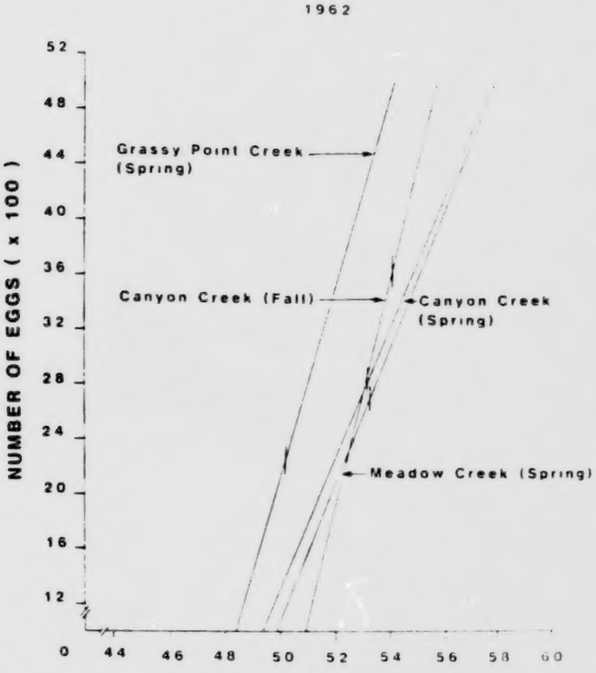

FIG. 6. Relationship of fecundity to length of sockeye salmon from selected spawning grounds of Karluk Lake, 1962. Vertical lines indicate the mean lengths and fecundities of females sampled.

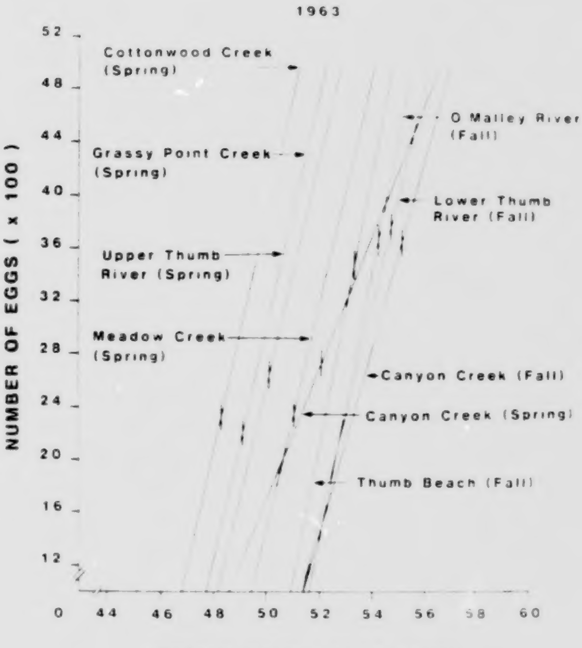

FIG. 7. Relationship of fecundity to length of sockeye salmon from selected spawning grounds of Karluk Lake, 1963. Vertical lines indicate the mean lengths and fecundities of females sampled.

nursery areas in the lake.[3] On several occasions, we observed large schools of fry ascending upper Karluk River during the day; i.e., they were positively rheotactic and phototactic. By contrast, most fry hatched in tributary streams migrate individually to the lake at night and face downstream; i.e., they are negatively rheotactic and phototactic (Hartman et al. 1967). Thus, migrating fry from tributary streams and upper Karluk River differ in schooling behavior, orientation to stream current, and diel timing.

Seasonal as well as diel differences in time of fry migration from individual spawning grounds seemed related to the time of spawning of the parent generations. In 1963, fry migrated from Grassy Point Creek in one wave between early April and mid-June, while fry migrated from Canyon Creek in two well-separated waves or periods of abundance between early April and late July (Fig. 10). In 1962, the parents of the Grassy Point Creek fry had spawned in one wave, while parents of the Canyon Creek fry had spawned in two waves. Presumably, the two waves of fry in Canyon Creek were derived independently and sequentially from the two waves of spawners. The difference of about 60 days between the peak of abundance of both the parent and progeny curves, and similar differences in abundance of parents and offspring in the two waves, support this view (Fig. 10).

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[3] A few Karluk River fry apparently migrate directly to the sea because a small number of river-type scales (i.e., 3_1, 4_1) have been recorded (Barnaby 1944).

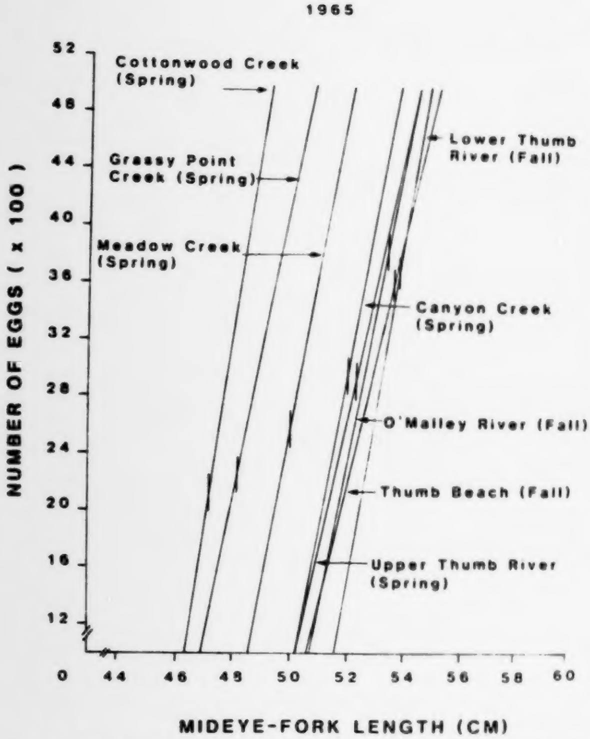

FIG. 8. Relationship of fecundity to length of sockeye salmon from selected spawning grounds of Karluk Lake, 1965. Vertical lines indicate mean lengths and fecundities of females sampled.

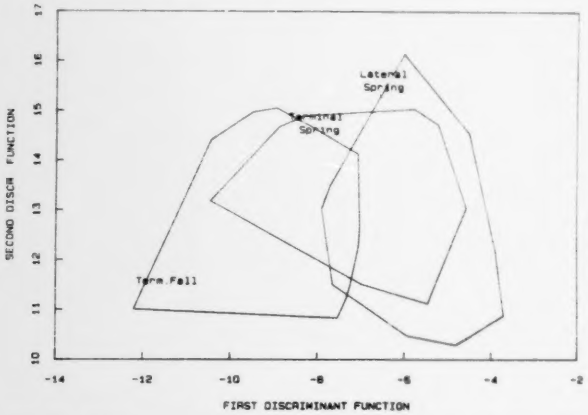

FIG. 9. Linear discriminant function analysis: convex polygons differentially delineating characteristics of three major spawning groups in the Karluk system as measured by the first and second discriminant functions.

Since significant (t; $P<0.01$) differences in the lengths of spawners in Grassy Point and Canyon creeks were demonstrated in 1962 and 1963 (Fig. 3 and 4), we wondered if size differences would also be evident at the fry stage. To answer this question, we obtained fork lengths of fry during the 1964 migration from Grassy Point Creek and during the first wave of the migration from Canyon Creek. Thus, the fry sampled in each creek were assumed to be derived from only the spring runs of spawners. Average length of fry from both creeks increased over the sample period as stream temperatures warmed (Table 4), an adaptive mechanism that may compensate somewhat for the shorter first growing season that would be experienced by later-emerging fry. Over the entire migration period, Canyon Creek fry averaged 0.9 mm longer than Grassy Point Creek fry, a significant (t; $P<0.01$) difference. This difference in length of fry in the two streams paralleled the difference in length of adult fish.

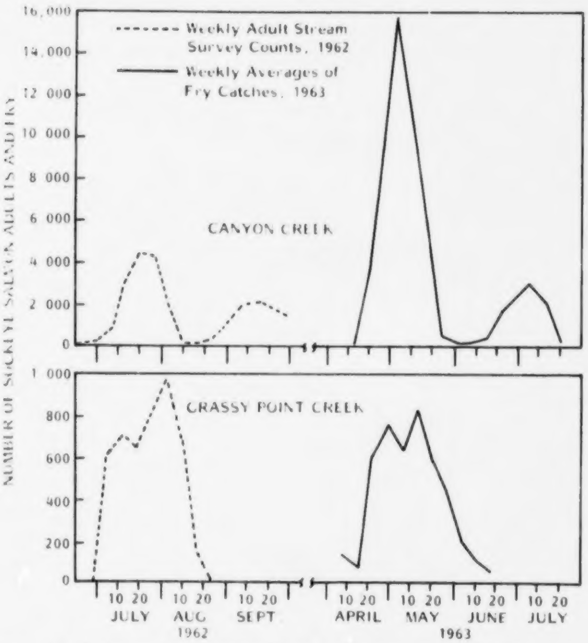

FIG. 10. Relation between time of parent spawning in 1962 and time of migration of fry in 1963 in Canyon and Grassy Point creeks. Fry catches shown are total numbers caught nightly in two nets (Grassy Point Creek) and three nets (Canyon Creek).

Discussion

Conditions necessary for the evolution of subpopulations are thoroughly treated by Mayr (1963). First, there must be genetic variability in the population. Commenting on genetic variability of salmonids, Svärdson (1945: 126) stated: "This variation of their(s) may be due to a comparatively lively re-arrangement of the gene material. This re-arrangement is most pronounced in the gwyniad (*Coregonus lavaretus*) which also reveals the most pronounced variation and racial diffusion." Surely the Karluk sockeye salmon also have a great reservoir of hereditary diversity. Second, a variable environment is helpful, though not essential, in the process of evolution. We have already pointed out a diversity in spawning habitats in the Karluk system. Third, there must be reproductive isolation. Groups of Karluk sockeye salmon have been shown to be reproductively isolated by season. Further, Hartman and Raleigh (1964) discovered that less than 3% of the Karluk sockeye salmon strayed between streams; hence, populations originating from different streams seem unlikely to be mixed at spawning time.

TABLE 4. Length of fry from Grassy Point Creek migration and from the first wave of the Canyon Creek migration, 1964.

Date	Number of fry		Mean fork length of fry (mm)	
	Grassy Point Creek	Canyon Creek	Grassy Point Creek	Canyon Creek
April 21	43	49	28.0	29.4
April 28	33	36	29.1	29.5
May 6–7	44	42	28.6	29.2
May 14	39	40	29.0	29.9
May 20	43	44	29.4	30.2
May 27–28	36	41	29.7	30.3
Total	238	252	28.9	29.8

Our analysis revealed physical and behavioral differences between groups, but did not distinguish between a genetical or environmental origin of these differences. Results of many salmon studies which bear on this problem have been evaluated by Ricker (1972). He concluded (page 145): "Since season of return to the river is strongly under genetic control, and ability to 'home' is apparently partly under genetic control, a corollary is that most or all of the identified stocks of these fish differ genetically to some extent." Also in relation to season of return and homing, Mayr (1963: 91) stated: "Isolating mechanisms always have a partially genetic basis." Ricker (1972: 68–71) demonstrated an effect of genetics on freshwater age of sockeye salmon smolts in Cultus Lake, while Godfrey (1958) reported that ocean age of Rivers Inlet and Skeena River sockeye salmon was governed to a great extent by heredity. Experimental evidence indicating some genetic control of size of kokanee was presented by Vernon (1957); moreover, on page 595 Vernon stated: "It is highly probable that similar genetic divergence has occurred between groups of sockeye." Svärdson (1949) concluded that within the same species an individual variation in hereditary capacity to produce eggs must occur. The direction of migration of sockeye salmon fry from inlet and outlet streams was found to be under genetic control (Raleigh 1967; Brannon 1969). Finally, Wilmot and Burger (1985) found statistically significant differences in allele frequencies of three enzymes between spring- and fall-run Karluk sockeye. On the basis of these many studies, we feel that at least part of each demonstrated character difference between groups of Karluk sockeye salmon probably is due to genetic differences.

The existence of subpopulations of sockeye salmon in Karluk Lake has also been considered by earlier workers. After analyzing timing and abundance of age groups, Rounsefell (1958) concluded that Karluk sockeye salmon were all of a single population [equivalent to the "subpopulation" of Marr (1957)]. He gave the following reasons: (1) seasonal modes of abundance could be caused by the seasonal pattern of life history types; and (2) numbers of early- and late-running 5_3's were correlated, as were 4_3's and 5_3's of the same year-class. Ricker (1972: 41) questioned this interpretation, stating:

> "As I see it, however, none of the information presented precludes the possibility of considerable discreteness of stocks arriving at different seasons, provided the stocks are distinguished by having different proportions of the different life-history types, as is actually the case (personal communication from Dr. J. B. Owen). The fact that different ocean groups (having the same number of fresh water years) vary in abundance in a similar fashion might reflect variations in survival conditions in the lake during their common freshwater life."

At the inception of the fishery, most of the sockeye salmon apparently spawned in midseason. Freshwater survival should favor both the midseason spawners and their progeny because midseason environmental conditions were most favorable (Thompson 1950; Rounsefell 1958). Why, then, under a single population hypothesis, aren't most of the fish still spawning at midseason instead of in the spring and fall? The most likely explanation, in our view, is that spring and fall run fish are genetically different and programmed to spawn at these specific times and, barring some straying, will continue to do so.

Evidence of a hereditary basis for direction of fry migration (Raleigh 1967), for the separation of spring and fall runs (Wilmot and Burger 1985), and for tributary homing (Hartman and Raleigh 1964) is consonant with possible genetic components for the character differences presented in this paper. All this evidence supports the hypothesis that the run of sockeye salmon to the Karluk River is composed of at least two subpopulations which segregate in fresh water by time and space.

Acknowledgments

We are indebted to the many summer employees who assisted in the field work, particularly, Robert Hurley, Kenneth Durley, Jerry Loll, Richard Haight, and John Brandon. Donald Seegrist, Joseph Greenough, Jerome Pella, and Galen Tromble assisted with the statistical analysis and Charles DiCostanzo advised on all phases of the investigation. William Ricker reviewed the manuscript and made many helpful suggestions concerning analysis of fecundity data and timing of the runs. We also acknowledge the report by Owen et al. (1962) from which some of the ideas pursued in this investigation originated.

We thank the University of Alaska–Juneau Research Council for support in processing this report and the University of Alaska Computer Network for furnishing computer resources.

We dedicate this paper to the memory of Dr. William Francis Thompson who was greatly interested in this study and encouraged the preparation of this report.

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An Aquatic Rubic's Cube: Restoration of the Karluk Lake Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

KOENINGS, J. P., AND R. D. BURKETT. 1987. An aquatic Rubic's cube: restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*), p. 419–434. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

The decline in abundance of sockeye salmon (*Oncorhynchus nerka*) in Karluk Lake since 1889 has been attributed to overfishing. Nearly 100 years later the puzzle of how overfishing forced the decline, and what now maintains production at $<10\%$ of historical levels remain unresolved. An explanation is suggested based upon results of a 7-yr (1979–85) intensive study of the freshwater rearing environment. Karluk Lake strongly influences each sockeye life history phase by: (1) partitioning the adult run into spring and fall spawners, (2) maintaining discrete adult sub-stocks with numbers that fluctuate independently, (3) maintaining different emergence times for fry from these discrete stocks, and (4) establishing the timing and magnitude of juvenile forage production. The mechanism causing the decline is seen as operating within the freshwater environment to change stock-recruitment relationships. Concurrent declines in lake fertility and sockeye populations impeded restoration efforts, and if the run is to recover, increased escapements must be accompanied by enhanced freshwater survival. Inconsistent freshwater forage production must be temporally stimulated through nutrient enrichment, in order for increased fry recruitment to produce larger adult runs.

Résumé

KOENINGS, J. P., AND R. D. BURKETT. 1987. An aquatic Rubic's cube: restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*), p. 419–434. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

On croit que la chute du nombre de saumon nerka (*Oncorhynchus nerka*) dans le lac Karluk depuis 1889 est le résultat d'une surpêche. Environ un siècle plus tard, la manière dont cette surpêche a entrainé le déclin et les facteurs qui maintiennent la production à $<10\ \%$ des niveaux historiques demeurent toujours un mystère. L'auteur présente une explication basée sur les résultats d'une étude intensive (1979–1985) des zones d'alevinage en eau douce. La forte influence du lac Karluk sur chaque stade du cycle vital du saumon nerka se manifeste par : 1) la séparation de la remonte en géniteurs de printemps et d'automne, 2) le maintien de sous-stocks indivuels d'adultes dont les effectifs fluctuent indépendamment, 3) le maintien de différents temps d'émergence des alevins appartenant à ces stocks individuels, et 4) l'établissement du moment et de l'importance de la production de nourriture pour les juvéniles. On considère que le mécanisme responsable du déclin a lieu dans les eaux douces et qu'il modifie les relations stock-recrutement. Les déclins simultanés de la fertilité lacustre et des populations de saumon nerka ont entravé les efforts de remise en état et, si l'on veut obtenir un rétablissement de la remonte, l'accroissement des échappées doit être accompagné d'une survie améliorée en eau douce. La production variable d'aliments en eau douce doit être stimulée temporellement par l'apport de bio-éléments de façon à ce qu'une amélioration du recrutement d'alevins accroisse les remontes.

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Introduction

Karluk Lake is today less famous for its once great sockeye salmon production than for loss of that production and the reasons for it. The decline of the run has two features common to many notorious scientific puzzles: first, the problem has been widely known for a long time (Bean 1891; Gilbert and Rich 1927; Juday et al. 1932) and second, there have been many efforts directed to its resolution (e.g., Barnaby 1944; Rounsefell 1958; Owen et al. 1962; Drucker 1970; and Van Cleve and Bevan 1973).

Rounsefell (1958), in particular, suggested many of the following alternative explanations for the puzzling decline of the Karluk Lake sockeye run:

1) Long-term changes in the physical environment (Rounsefell 1958),
2) Increased predation of juvenile sockeye during lake residence (Rounsefell 1958),
3) Blockage of Karluk River preventing fry from reaching the lake (Van Cleve and Bevan 1973),
4) Overfishing the run in general (Bean 1891; Barnaby 1944; Rounsefell 1958),
5) Selective overfishing of one or more discrete populations in the Karluk run (Owen et al. 1962),
6) Reduction in lake fertility (Barnaby 1944).

While the fourth, and more recently the fifth alternative has been generally accepted as the cause of the decline (Bean 1891; Owen et al. 1962), the destructive mechanism(s) is not yet understood. Gaining this understanding is of more than academic interest if the run is to be restored. However, as there can be little doubt that the Karluk Lake fish community must be fundamentally different in both composition and interrelationships from that of nearly a century ago (Larkin 1977), we recognize that restoration may require strategies other than simply treating what caused the decline. Our approach focuses on the freshwater rearing phase and its role in smolt production rather than on the manipulation of escapements. We draw upon the pioneering limnological studies of Juday et al. (1932) and extensive work on juvenile sockeye dynamics by Barnaby (1944) to identify the probable mechanism for the decline and recommend procedures to bring it back to historical abundance.

Study Area

Karluk Lake is a clearwater lake lying on the southwest end of Kodiak Island, Alaska (57°24′N; 154°05′W). It has a surface area of 39.5 km^2, and a mean depth of 48.6 m (Juday et al. 1932). The maritime climate, average annual precipitation of 172 cm and large (282 km^2) watershed result in a water residence time of only 4.8 years. Numerous lateral streams drain the watershed mountains and two smaller lakes, Thumb (1.06 km^2) and O'Malley (2.15 km^2), drain into two upper arms.

Karluk Lake is oligotrophic with a mean euphotic depth reaching 23 m, mean May–October total phosphorous concentrations equalling 7.8 mg/m^3, chlorophyll *a* levels averaging 2.5 mg/m^3, and a macrozooplankton community consisting of *Bosmina longirostris*, *Daphnia longiremis*, *Epischura nevadensis*, *Diaptomus pribilofensis*, and *Cyclops columbianus*. The lake has three basins (Table 1), each with distinctive physical features, that serve as juvenile nursery areas. Thus, the lake does not constitute a homogeneous rearing environment, as also evidenced by two underpopulated basins (Thumb, O'Malley) relative to numbers of juveniles using the Main basin. Little correlation was observed between the physical features of the basins and fish densities (FD) except littoral area (LA): $\%LA = 12.29 + 0.61 (\%FD)$; $r^2 = 0.97$. The lower Main basin is almost separated from the two upper basins by a narrow glacial moraine, 5 m below the surface, midway up the lake. For a more detailed description, see Gilbert and Rich (1927), and Juday et al. (1932).

Materials and Methods

Limnological studies of the Karluk Lake sockeye nursery were designed to characterize the three lake basins at 3-wk intervals from ice-off in the spring to ice-on in the winter and on 1–3 occasions during the winter. Lake temperature and light penetration were measured at a minimum of three permanent stations using a YSI temperature/dissolved oxygen model 57 meter and a Protomatic submersible photometer, respectively. Measurements were taken at 1-m increments from the surface to 5 m, at 2-m increments from 6 to 12 m, and at 10-m increments from 20 to 100 m. The algal light compensation point was defined as the depth at which 1% of the subsurface light (400–700 nm) is available for photosynthesis (Schindler 1971).

Both the epilimnetic and mid-hypolimnetic zones were sampled for algal nutrients (e.g., nitrogen, phosphorus, silicon, and carbon) and other water quality characteristics. All chemical and biological samples were analyzed according to procedures detailed in the Alaska Department of Fish and Game limnology manual (Koenings et al. 1987b). Filterable reactive phosphorus (FRP) was analyzed by the molybdate blue-ascorbic acid method of Murphy and Riley (1962) as modified by Eisenreich et al. (1975). Total

TABLE 1. The physical characteristics of the three major basins (Thumb, Main, and O'Malley) of Karluk Lake that define different rearing conditions for sockeye juveniles.

Limnological station	Basin	Surface area ($m^2 \times 10^{+6}$)	Volume ($m^3 \times 10^{+6}$)	Littoral area ($m^2 \times 10^{+6}$)	Mean depth (m)	Water residence time (yr)	Light compensation point (m)	Mean juvenile density (Jul.–Sept.) (% of total)
2	Thumb	4.3(11%)	116(6%)	1.3(17%)	27	1.3	23	3
3	Main	15.1(38%)	471(25%)	4.2(55%)	31	3.7	25	66
4	O'Malley	20.1(51%)	1 333(69%)	2.1(28%)	66	7.1	21	31
	Karluk	39.5(100%)	1 920(100%)	7.6(100%)	48.6	4.8	23	100

[2] Mean of 1983–85.

phosphorus was determined by the FRP procedure after persulfate digestion. The procedure of Strickland and Parsons (1972) was used in the analysis for reactive silicon (Si) levels.

Primary production (algal standing crop) was estimated by chlorophyll *a* (chl *a*) analysis using the fluorometric procedure of Strickland and Parsons (1972). We used the low strength addition recommended by Reimann (1978) to estimate phaeophytin. Water samples (1–2 L) were filtered through 4.25 cm GF/F filters to which 1–2 mL of saturated $MgCO_3$ solution were added just prior to completion. Filters were stored frozen in separate plexislides for later analysis.

Zooplankton were enumerated from duplicate 50-m or bottom-to-surface vertical tows using either a 0.2-m or 0.5-m diameter, 153-μm mesh, conical zooplankton net. The net was pulled at a constant 1 m/s, and washed well before removing and preserving the organisms in 10% neutralized formalin solution. At least three permanent stations were sampled 6–8 times during the open water period. Zooplankton of the genus *Daphnia* and *Bosmina* were identified according to Brooks (1957) and Pennak (1978), respectively, and copepods, as described by Wilson (1959), Yeatman (1959), and Harding and Smith (1974). Zooplankton were counted in triplicated 1-mL subsamples taken with a Hensen–Stempel pipette and placed in a 1-mL Sedgewick–Rafter cell.

Juvenile sockeye distribution and abundance in the lake were estimated with a 70 KHz Simrad EYM echo-sounder and Sony cassette recorder. A downward-looking 11 degree transducer was suspended from the bow of the boat. Open water trawls with a 2 × 2 m tow net (Gjernes 1979) were used to identify hydroacoustic targets. Ten replicate cross-sectional tows were usually conducted along the entire longitudinal axis of the lake except for diel studies where single cross-sectional transects were used in each of three basins. Surveys were conducted in the spring, summer, and fall periods. The data were analyzed by echo integration (Nunnallee 1980) using a Biosonics model 120 digital integrator. Other information pertinent to juvenile growth and emergence was obtained from Gard and Drucker (1963), Hartman et al. (1967), and DiCostanzo (1972). Estimates of smolt numbers were obtained from Barnaby (1944), Rounsefell (1958), Drucker (1970), and from White (1987) who describe the methods used in detail. Ages, numbers, and timing of adult spawners were obtained from Bean (1891), Gilbert and Rich (1927), Barnaby (1944), Drucker (1970), and from White (1987).

Results and Discussion

THE PUZZLE

Karluk Lake sockeye salmon production (catch + escapement) has dropped precipitously from an estimated 5.6 million fish in the 1890's to early 1900's to settle at around 500 000 adults over the past 35 years (Fig. 1). The initial cause of the decline of the Karluk sockeye was probably overfishing, especially of the middle segments of the run which may have contained more productive age-groups. In all likelihood, these age-groups had characteristic ocean and freshwater ages, and perhaps occupied unique habitats. In any case, management efforts aimed at enhancing the run, either by ensuring mandatory escapement levels (White Act 1924), or by fishing particular segments of the run (Barnaby 1944; Gard and Drucker 1965; Van Cleve and Bevan 1973) were unsuccessful. If a highly productive adult segment was reduced by overfishing, one would expect that the run would have responded to 65 years of management efforts to increase escapement, unless changes in the lake environment have also occurred to adversely affect fry growth and survival. Such changes could not be alleviated just by increasing escapements.

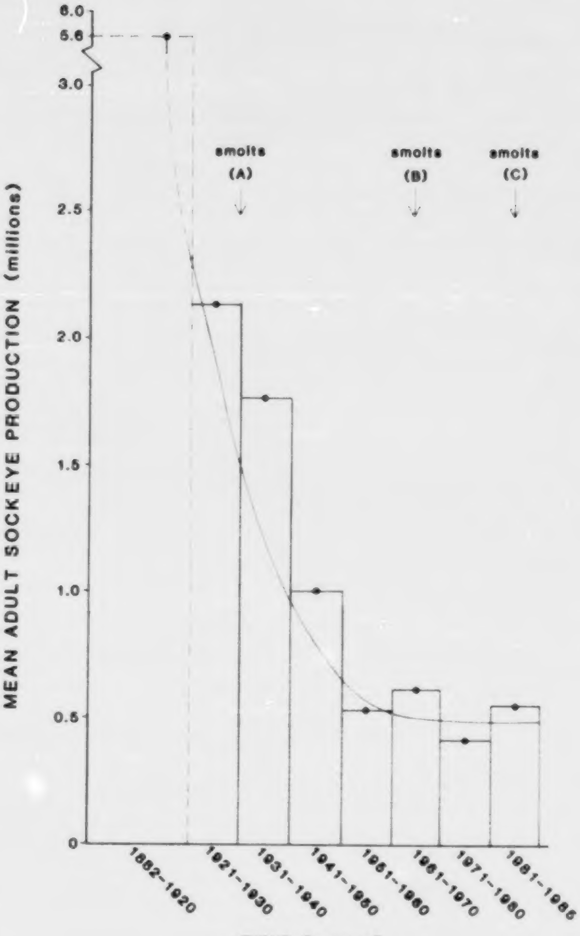

FIG. 1. The historical pattern of adult sockeye production from Karluk Lake showing the exponential decline (●) beginning in the late 1890's to the present plateau. In addition, the periods of intensive studies on emigrating smolts are indicated; period (A) refers to studies by Barnaby (1944), period (B), to those by Drucker (1970), and period (C), those by White (1987). Dashed lines indicate the less well-defined total adult return estimates of the early period at Karluk (Rounsefell 1958).

Considerable evidence from several Alaskan lakes, including Karluk, indicates that the freshwater, rather than the marine environment usually places upper limits on the numbers of returning adults (Burgner et al. 1969). Thus, environmental factors which control freshwater age and/or growth could have considerable impact on production of

Karluk sockeye salmon. In fact, freshwater age is inversely correlated with freshwater survival (Rounsefell 1958), and the combination of fry recruitment to the lake limnetic zone, and their subsequent survival could determine stock strength. Accordingly, Owen et al. (1962) concluded that some unknown factor(s) in the freshwater environment has held the run down.

In contrast to this reasoning, for over 65 years studies to determine the cause of the decline of the sockeye salmon run at Karluk Lake have emphasized the location, timing, and magnitude of the adult escapement. As a result, it is well recognized that groups of Karluk Lake spawners utilize distinct locations and have characteristic age compositions. The precept developed that when a fishery operated on these groups selectively, the most productive ones were preferentially reduced in abundance (Larkin 1977).

The subunit concept was not coupled with changes in the lake because of the prevailing thought that "groups of salmon would tend to be affected in common by environmental factors such as those encountered during common brood year and during lake residence" (Owen et al. 1962). A common lacustrine environment could not produce the observed and very real changes in sockeye subpopulations within the system (Barnaby 1944).

We believe that the lack of correspondence between numbers in escapements and returns is due to both a variable lake environment and fluctuations in fry recruitment timing, the latter attributed to the timing and age composition of spawners. The relative synchrony of fry emergence with the lacustrine food supply and the duration of intra-annual rearing determine the relative survival of subpopulations of fry.

Our object is, therefore, to concentrate on the freshwater environment as suggested by Barnaby (1944) and Owen et al. (1962). To do this, we must first understand the relationship between the abundance of fry and the abundance of adults.

AGE COMPOSITION AND SPAWNING CHRONOLOGY

Three hypotheses exist on the relationship between the stock composition of the overall Karluk sockeye run and spawning times:

1) Gilbert and Rich (1927) and Barnaby (1944) both recognized the general existence of separate stocks because of spawning times that clearly produced a bimodal (spring and fall) spawning distribution,
2) Rounsefell (1958) argued in favor of only a single stock having a unimodal distribution that was obscured by fishing pressure to reflect an apparent bimodal distribution, and
3) Thompson and Bevan (1954), Owen et al. (1962), and Van Cleve and Bevan (1973) rejected Rounsefell's (1958) arguments of a single stock (and the subsequent use of a single spawner–recruit relationship), but retained the concept of a unimodal spawning distribution modified by fishing pressure to yield a bimodal distribution.

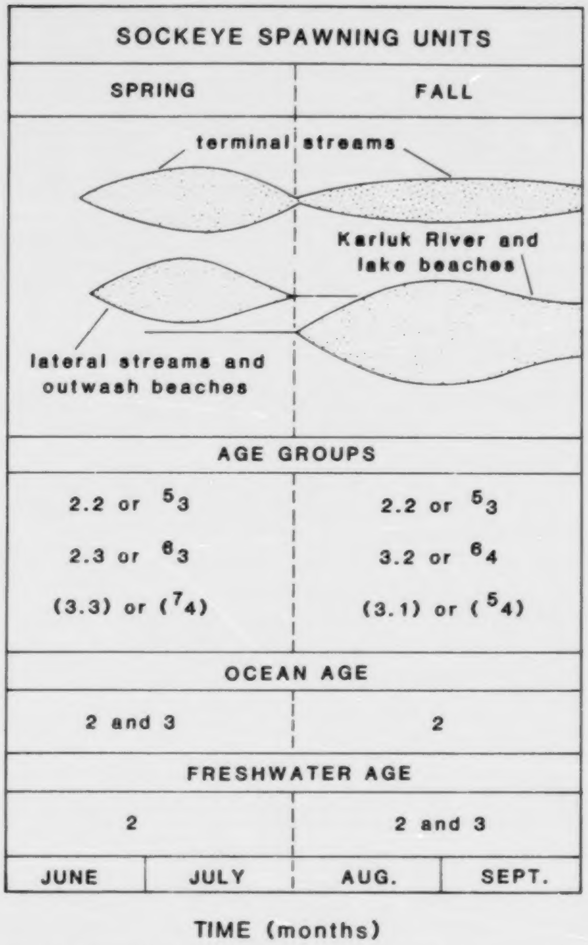

FIG. 2. Generalized schematic of the major sockeye spawning stocks and characteristic spawning sites during the time of active spawning. Spring (early) spawners are primarily age 2.3 and 2.2 whereas fall (late) spawners are primarily age 3.2 and 2.2. Both spring and fall spawners share the 2.2 age the often dominant, mid-season spawning group in the overall escapement. Other adult age-groups included within parentheses are, at times, important contributors to the overall run. Spawning by the spring run generally peaks in early to mid-July followed by a period of little or no spawning in early August and then a second surge of fall spawners peaking in September [after Gilbert and Rich (1927), Barnaby (1944), Owen et al. (1962), and Drucker (1970)].

Our analysis supports the first hypothesis for the following reasons. The overall sockeye run to Karluk Lake comprises several subpopulations (stocks), freshwater age-groups, and ocean age-groups, which arrive on the spawning grounds at different times (Fig. 2); and in different numbers. For example, the earlier spawning, 2.3 fish are characteristic of the spring run, and predominantly enter the lateral or terminal streams to spawn. In contrast, the 3.2 fish enter the spawning grounds later and spawn, predominantly, in Karluk River or on the lake beaches (Owen et al. 1962). Of particular importance are the 2.2 adults which are found at all times during the run, i.e., they are represented in both the fall and spring spawning segments. Overall, both the spring and fall runs produce 5 and 6 yr-old adult salmon, but only the 2.2 age-group is produced in quantity by both runs (Fig. 2). Because of a central tendency in spawning times relative to the two extremes established by the earlier (2.3 group) and later (3.2 group) spawners, both components of the 2.2 age-group have been collectively labelled the "mid-season" spawners. However, while having the same age designation, the 2.2 fish need not spawn as a homogeneous group (i.e., in a unimodal pattern), but, in fact, spawn as a more heterogeneous group as members of both the spring and fall spawners (i.e., in a bimodal pattern).

The pattern wherein early (spring) spawners favor streams and some late (fall) spawners utilize beaches is not unique to Karluk. In the Russian River system (Cook Inlet), spring-run (late June) fish are predominantly age 2.3 and spawn in Upper Russian Creek while the fall-run (late July) fish are predominantly age 2.2 and spawn almost exclusively on the Upper Russian Lake beaches (Nelson 1985). Similar spawning distinctions are observed between spring and fall spawners in Chignik and Black Lakes (Alaska Peninsula).

Brannon (1984) suggests that stocks are genetically adapted to their environment with the driving force for different spawning times in different streams being respective water temperature regimes. That is, the colder the incubating water (e.g., spring fed inlet creeks), the sooner eggs need to be deposited for fry to emerge at the proper time in the subsequent spring. Indeed Dirin-Khalturin (1981) argued that the temperature of the spawning area is the primary basis of ecological differentiation in salmon, i.e., for the divergence of species and the appearance of seasonal races.

Genetically separate races are not essential to the existence of different recurring patterns of fry emergence timing. The key requirement is that each characteristic spawner group occupy the same habitat during the same calendar periods every year. This constancy allows a genetic adaptation promoting optimum survival of each group, i.e., most sockeye fry enter lakes when environmental opportunities are most favorable for their growth and survival. In general, entry coincides with the start of the growing season when lake water temperatures rise and zooplankton blooms (Hartman et al. 1967; Foerster 1968; Brannon 1984). Eventually groups adapt to local incubation temperatures and emerge at the optimum time (Dirin-Khalturin 1981). Once this pattern is established a site specific temporal regularity in spawning occurs. In the Fraser river system sockeye spawners exhibit an inter-annual variation around the mean date of emergence of about ± 10 days (Brannon 1984).

Consistent spawning time (Figure 2) is also a basic characteristic of the Karluk Lake run (Owen et al. 1962). This has persisted in the periods reported by Gilbert and Rich (1927), by Drucker (1970) and continues today. For instance, Barnaby (1944) and Owen et al. (1962) described the Karluk spawning grounds as virtually unoccupied during late July to early August, i.e., between the spring and fall spawnings. Gilbert and Rich (1927), Conkle et al. (1959), Gard and Drucker (1963), and DiConstanzo (1972) reported little spawning between 25 July and 20 August, thus, establishing the bimodal nature of the spawning over many decades.

This distinct bimodality on the spawning grounds is less definite in the fishery and at the weir. For this reason, Barnaby (1944) suggested that the mid-season low abundance of spawners was due to environmental conditons in the lake, and we agree. We have found that the time of maximum water temperature in Karluk Lake acts as a thermal stimulus or focus to separate spring from fall spawning stocks. Specifically, we have observed that during 1979–85 Karluk Lake has accumulated the maximum number of calories/cm^2 between 25 July and 16 August with a mean at 5–6 August. Historically, as early as 1927, Juday et al. (1932) reported a similar timing for the maximum heat of the lake. The variation in maximum heat content is similar to the inter-annual variation in spawning times for the Fraser system reported by Brannon (1984). Simply put, the spring run spawns in colder water as temperatures rise while the fall run spawns in warmer water as temperatures fall. Thus, water temperature, so important to the life history strategies of poikilotherms may be maintaining a bimodal spawning distribution.

SYNCHRONY OF FRY EMERGENCE WITH FORAGE PRODUCTION

As spawning times of particular stock units appear to be controlled by temperatures at respective spawning sites, fry growth and survival in freshwater may differ among units depending on the degree to which fry emergence is synchronized with important seasonally defined rearing conditions in the lake. This key concept was not recognized by Barnaby (1944), Rounsefell (1958), or Owen et al. (1962) because they believed that "a change in environment that would increase or decrease the mortality of the fingerlings in the lake should affect each age group of seaward migrants in a similar manner. No data are at hand to indicate that environmental conditions have altered in such a manner as to affect the mortality of one age group without affecting the mortality of the other age group".

Until recently, drastic asynchrony in timing of fry emergence and forage production would have gone unnoticed because studies were conducted only from June through August, when forage production within the lake was very stable (Juday et al. 1932). An early hint of variation in within year fry forage production came as an incredulous aside by Hilliard (1959) who cryptically noted that "in Alaska it would appear that biologists, principally those concerned with fisheries, are predisposed to a priori reasoning that biological productivity is nil during the late fall or winter". He cited the work of Juday et al. (1932) who used a two-month period during the summer (16.7% of the year) as "the sole basis of determining lake productivity as related to salmon fisheries". Hilliard (1959) found that during the summer months (as defined by Juday's studies) *Cyclops scutifer* [presently classified as *Cyclops columbianus* (Bowman 1983)] averaged 0.6 organisms/L compared to over 11 organisms after the summer months and until freezeup. He concluded: "it is apparent from the available data that sampling over such a limited period can give misleading concepts of plankton populations". The relationship between times of stock spawning and fry emergence was initially addressed by Hartman et al. (1967), but they assumed that forage production began in the spring and did not extend beyond the summer months. This perpetuated the idea that the juvenile rearing period at Karluk also begins in the spring, and that a temporal synchrony exists only between a spring bloom in forage production and early emerging fry.

Gard and Drucker (1963 and 1965) investigated the relationship between the seasonal timing of adult spawners and the emergence times of the fry. Over a period of 4 yr they clearly demonstrated the consistent times of spawning of spring and fall run fish and the equally consistent fry emergence times; fry from spring spawners began emerging from mid-April to early May while fry from fall spawners emerged by late June or early July, an 8–10 wk difference. Hartman et al. (1967) and DiCostanzo (1972) also believed that the initial entry of fry from tributary creeks into Karluk Lake occurred in the same two periods.

Initially, Hartman et al. (1967) assumed that survival of the late migrants was reduced by virtue of a slower growth rate resulting from later entry into the rearing areas. Our recent work on the seasonality of fry forage production suggests that it would be earlier emerging fry that survive less well. As Hilliard (1959) suggested, we found that most zooplankton production occurs during the fall-winter period (Fig. 3). Considering the average production during May to November as a base, the actual macrozooplankton population in Karluk Lake would be below average during May through July, and above average during August through November. Thus, stocks that produce earlier migrating fry would tend to be less productive per spawner than those that produce later migrating fry if synchrony with forage production is the principal factor. Moreover, the fecundity of fall spawners is thought to be greater than spring spawners of the same ocean age because of their greater average length. This also favors higher production per fall spawner (Hartman and Conkle 1960; Gard and Drucker 1965).

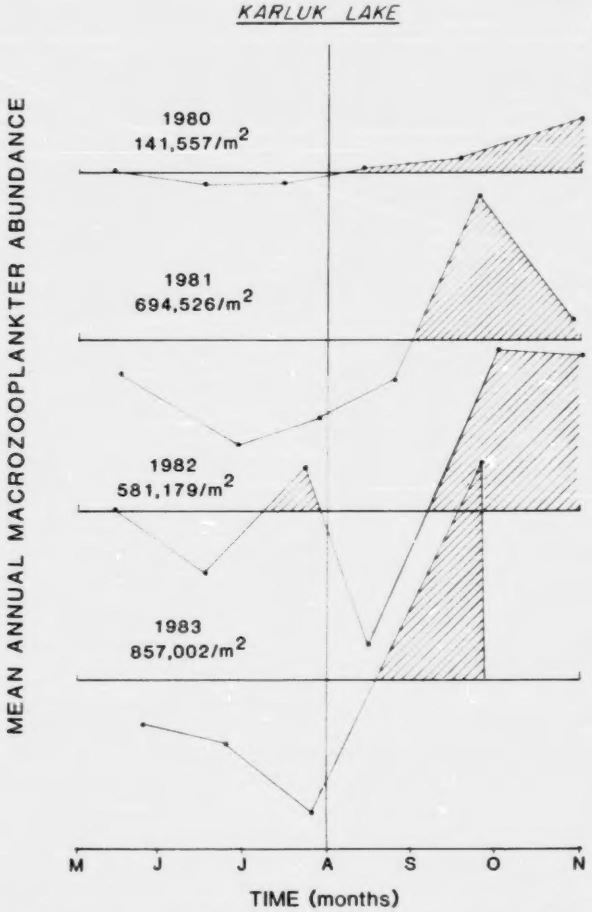

FIG. 3. The seasonal (May–October) timing of macrozooplankter production at three stations in Karluk Lake over the 1980–83 period. Solid horizontal lines indicate mean density over the season; individual points within a year show the actual density estimates.

A shift from predominantly age 2. to age 3. smolts was noted by Barnaby (1944) and might have resulted from improved survival of progeny of the more fecund fall spawning fish (many of which are age 3.2) (Fig. 2), rather than from a tendency for juveniles to remain in freshwater for an additional year in response to unfavorable rearing conditions. This shift could have been exacerbated if the fishery selectively harvested adults of the spring spawning stock since these fish are predominantly age 2. For example, Bean (1891) reported that as early as 1889 the Karluk spring spawning stock was virtually absent when adult fish first entered the river in August. Continued low spring production may have affected both the number of fry recruited and their subsequent survival in fresh water, and could explain the precipitous decline in the spring run to Upper Thumb River, once a major component of the Karluk run (White 1987). Indeed, we view this unproductive spring period to be responsible for the extremely low (< 1%) fry survival of Karluk fry both historically (Gilbert and Rich 1927; Barnaby 1944), and in the modern era (Drucker 1970). Equally as important, these factors (small escapements and low forage) operating in the freshwater phase, would impede the ability of managers to improve adult production simply by manipulating escapements.

For sockeye systems in general, Foerster (1968) found the period of spring synchrony of fry entry and forage production to be very critical, when mass mortality could occur. Such mortality could cause low correlation between escapements and resulting adult returns. Hartman et al. (1967) and DiCostanzo (1972) realized not only the importance of ensuring adequate escapements during all portions of the Karluk run, but also that the success of the resultant recruits was "strongly influenced by conditions that prevail in the environment at the time fry emerge from the gravel". Puzzled by the failure of the spring component of the 2.2 age-group at Karluk, Gilbert and Rich (1927) questioned: "Was there a scarcity, during the growth of this brood, in the pelagic organisms on which the red salmon almost exclusively feeds, a scarcity that caused extensive mortality among the colony and stunted the growth of those that survived?" In addition, LeBrasseur et al. (1969) found that in the very early stages of sockeye fry growth in Great Central Lake, mortality is heavy; but that abundant, readily available food of the optimum size increases their survival rate. Moreover, Burgner (1964), Johnson (1965), and Koenings and Burkett (1987) argue that as the growth rate of juvenile fish increases, the freshwater survival rate also increases.

Thus, the productivity of individual stocks at Karluk probably depended upon the numbers and composition of their respective escapements, and upon the time of emergence of the resulting juveniles relative to the timing and magnitude of forage production.

THE FERTILITY OF THE REARING ENVIRONMENT

Barnaby (1944) reported a temporary increase in the abundance of age 3., relative to age 2., smolts. However, he saw no related change in ocean ages of adults. He inferred that the fertility of Karluk lake was dropping because of reduced adult escapements. This supported the hypothesis of Juday et al. (1932) regarding the importance of carcasses in maintaining suitable conditions for juvenile growth. Rounsefell (1958) re-analyzed the Karluk Lake data and totally discounted Barnaby's hypothesis regarding changes in fertility. His arguments centered on three separate points: (1) that the amount of the critical nutrient, phosphorus (P), had not changed in the lake; (2) that the reported contribution of P from spawning streams due to salmon carcasses was incorrect, and that even if it were true, this contribution was insignificant relative to the contribution from other sources; and (3) that the relationship between numbers and biomass of Karluk smolt migrations is strictly linear indicating that intra-specific competition for food has not occurred.

We do not agree with Rounsefell's reasoning: First, using nutrient analysis procedures comparable to those used in the past, we found large annual variations in P levels 1979–82 and an overall decline (Fig. 4). In addition, it was evident that time of sampling was extremely important in any comparison of Karluk Lake total P levels; for example, the June–July samples revealed lower concentrations than did those of August–September. Nonetheless, when historical and recent measures are compared, the same seasonal nutrient cycle is evident. Rounsefell (1958) did not recognize the seasonal P cycle, and furthermore, he used an analysis procedure (phosphorus in a water residue test) that was not comparable.

Second, we compared levels of soluble P in Moraine and Halfway Creeks (Fig. 5), and Cascade and Meadow Creeks, and found that historically, P levels were many times higher than at present. Moreover, in recent years the peak P level each year following decomposition of adult carcasses was much less pronounced than historically, or a peak did not occur at all. A similar comparison of recent and historical patterns of reactive silicon levels revealed little variation within or between years. Unlike P, reactive Si is not a component of salmon carcasses, and the existence of different patterns for these elements implies that the decrease in P levels is not due to a general decline in nutrient levels in the watershed. Finally, peak P levels are positively correlated with numbers of sockeye salmon passing through the Karluk River weir, although the relationship is non-linear (Fig. 5). Thus, Rounsefell's (1958) argument that lower upstream and higher downstream P levels were caused by stream flow changes, not salmon carcasses, is not supported.

Rounsefell (1958) used the P data reported in Juday et al. (1932) and Barnaby (1944) to construct a P input model for Karluk Lake (Table 2). He then invoked these values in suggesting that the inflow from the tributaries, without the contribution from salmon carcasses, was double the input from as many as one million spawners. In that case, the observed reduction in spawners would be unimportant as it would cause only a 10–15% decrease in lake P over a 75-yr period (Rounsefell 1958). However, the values used for total P in

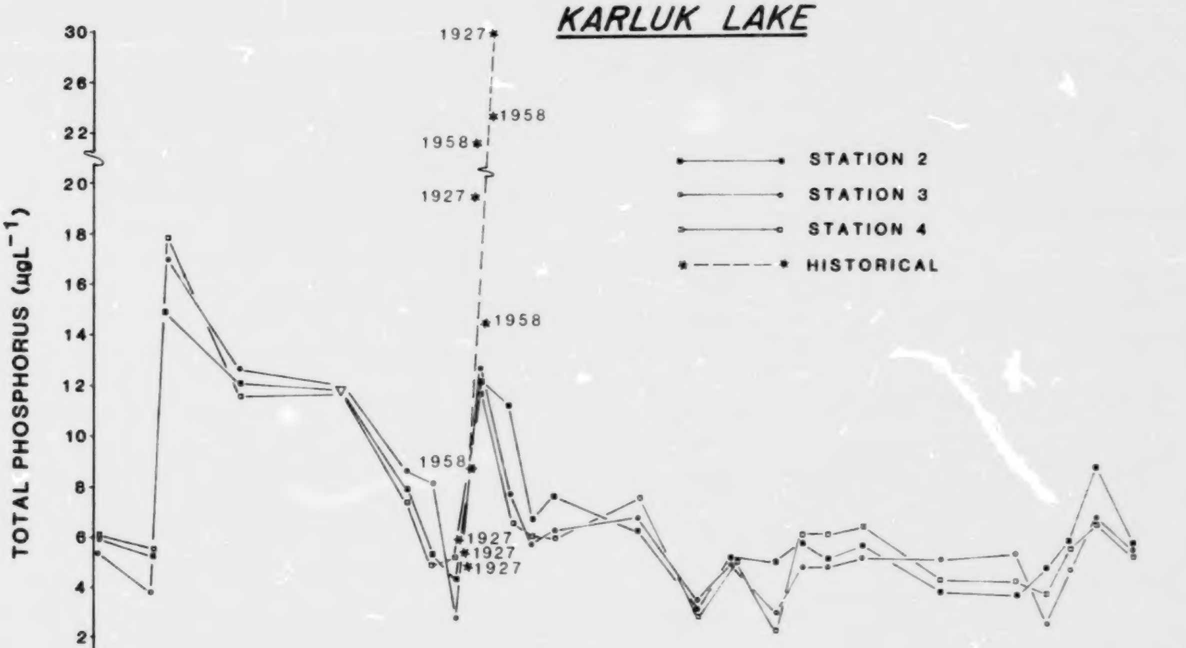

FIG. 4. Comparion of the recent (1979–82) annual variation in phosphorus concentrations at three stations in Karluk Lake with those from similar stations in both 1927 (Juday et al. 1932) and 1958 (Conkle et al. 1959). The open triangle indicates the P level at the one station successfully sampled in the spring of 1980.

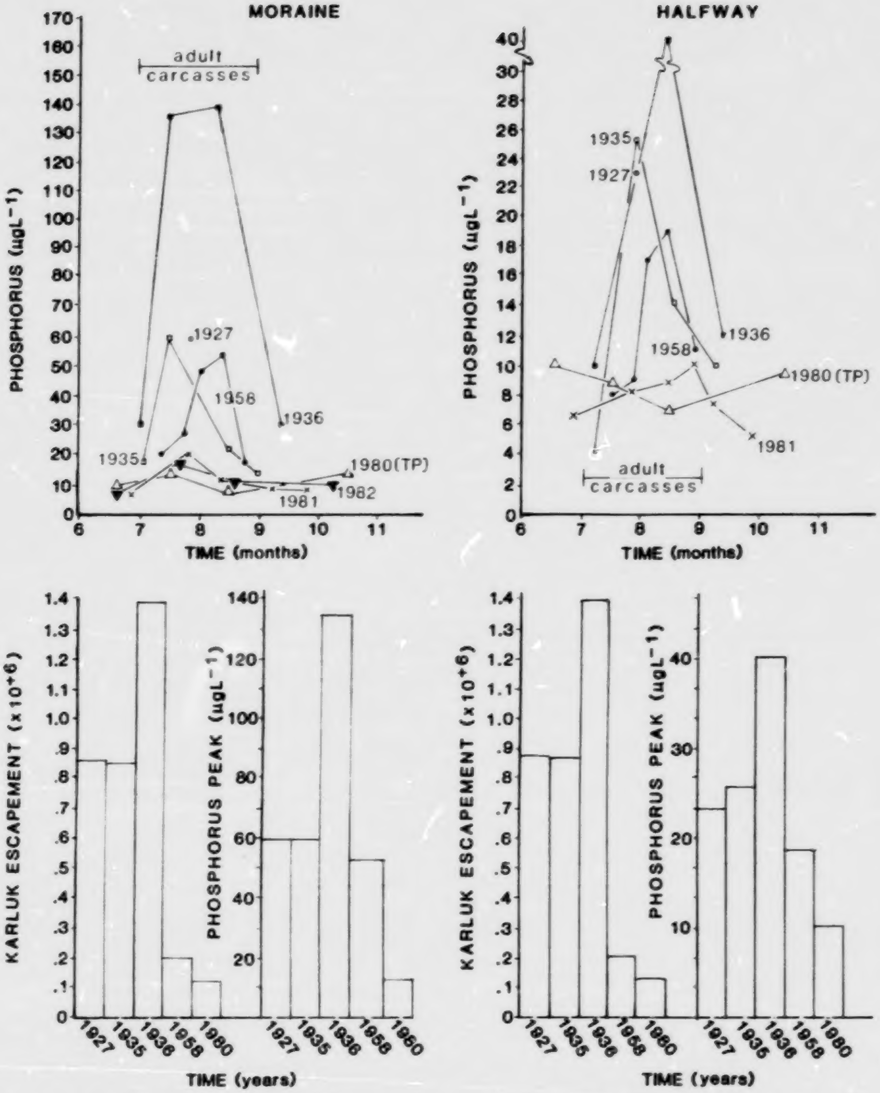

FIG. 5. Phosphorus levels in Moraine and Halfway Creeks, Karluk Lake, in 1927 (Juday et al. 1932), 1935–36 (Barnaby 1944), and 1958 (Conkle et al. 1959) compared to levels in 1980–82 (above), and the number of adult sockeye entering the lake relative to peak phosphorus levels in the streams (below).

TABLE 2. Phosphorus input calculations for Karluk Lake from Rounsefell (1958) corrected for computational errors and improved by inclusion of recent additions of relevant data.

Phosphorus source	Rounsefell (1958) Original (kg)	Rounsefell (1958) Corrected (kg)
Estimated in Karluk Lake water	31 680	10 176
Estimated annual inflow from tributaries	11 480	5 622
Estimated annual gain from 1 000 000 carcasses	6 100	8 074
Total	49 160	23 872

the lake came from residue samples of Juday et al. (1932) which were over 3 times the P indicated by an analysis procedure equivalent to that used for the stream samples. If the appropriate Karluk Lake P levels in Juday et al. (1932) are used, the estimate of total lake P is reduced by 68% to 10 176 kg. Recent data also show that Rounsefell's (1958) estimate of lake outflow (562 ft^3/s) was too high, which further reduces the terrigenous contribution by 36%. Moreover, this overestimate was compounded by a conversion error (17.5 mg $P/m^3 \times 656 \times 10^6$ ft^3/yr) which was used to estimate inflow from tributaries at 11 480 kg P/yr. The correct conversion is 17.5 mg $P/m^3 \times 502 \times 10^6$ m^3/yr or 8 785 kg P/yr which, reduced by an additional 36%, yields a value of 5 622 kg P/yr from the tributaries. Finally, the estimated contribution of P from one million carcasses was too low;

sockeye adult carcasses average 0.3364% (our data) or 0.3648% P (Donaldson 1967) or nearly 8–9 g P/fish for 2.4 kg sockeye, which implied a total P input from one million carcasses of between 8 074 kg/yr and 8 755 kg/yr.

Recent studies of Vollenweider (1976) and Smith (1979) have shown that it is the annual loading or renewal of P which is important in determining lake fertility. As one million sockeye carcasses generate about 8 000–9 000 kg of P annually, nearly 60% of Karluk Lake annual P loading comes from fish carcasses and contributes 4.7 mg P/m^3 to the P concentration. Krokhin (1967) estimated that salmon carcass decomposition would need to add at least 1.3 mg P/m^3 to a lake in order to stimulate productivity. Finally, since Gilbert and Rich (1927) noted that "there were spawned out humpbacks at every place where we landed around the lake", the potential contribution of P from pink salmon carcasses which numbered over four million 1.4 kg fish in the early 1900's would add nearly 19 000 kg more P to the Karluk system. Current input from pink salmon (1976 to 1986) is estimated at about 2 400 kg.

Fish P loading (L_f), a subfunction of the annual terrigenous or watershed related P input (L_p), changes in magnitude among lakes (Fig. 6) and years (Koenings et al. 1985b). This accounts for the well-known differential fertility of lake systems. However, since L_f and L_p can rise and fall independently, a drop in L_f can be made up by a rise in L_p, and oscillations in lake fertility can arise not only by changes to either L_f or L_p. A major portion of lake P loss

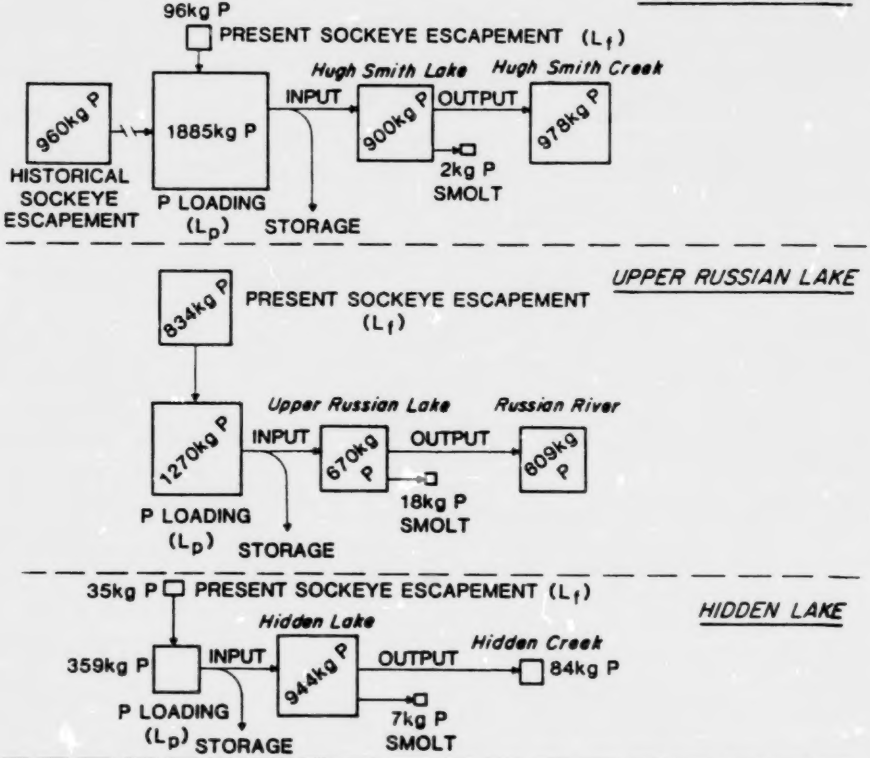
HUGH SMITH LAKE
96kg P
PRESENT SOCKEYE ESCAPEMENT (Lf)
960kg P
HISTORICAL SOCKEYE ESCAPEMENT
1885kg P
P LOADING (Lp)
INPUT
STORAGE
Hugh Smith Lake
900kg P
OUTPUT
Hugh Smith Creek
978kg P
2kg P SMOLT
UPPER RUSSIAN LAKE
834kg P
PRESENT SOCKEYE ESCAPEMENT (Lf)
1270kg P
P LOADING (Lp)
INPUT
STORAGE
Upper Russian Lake
670kg P
OUTPUT
Russian River
809kg P
18kg P SMOLT
HIDDEN LAKE
35kg P
PRESENT SOCKEYE ESCAPEMENT (Lf)
359kg P
P LOADING (Lp)
INPUT
STORAGE
Hidden Lake
944kg P
OUTPUT
Hidden Creek
84kg P
7kg P SMOLT
CRESCENT LAKE
783kg P
PRESENT SOCKEYE ESCAPEMENT (Lf)
9493kg P
P LOADING (Lp)
INPUT
STORAGE
Crescent Lake
1840kg P
OUTPUT
Crescent River
6135kg P
8kg P SMOLT

FIG. 6. Compartmental model of yearly phosphorus (P) budgets for several Alaskan sockeye nursery lakes comparing the magnitude of P inputs from fish carcasses (L_f) and terrigenous (L_p) sources to the P content of the lake; and to P outputs in smolts and the outlet discharge.

is via the outlet (Fig. 6), and when coupled with consistent decreases in L_f, it becomes the major cause of decreased lake fertility. Rounsefell (1958) assumed a response time of 75 yr (from input to loss via flushing) when refuting the importance of decreased P loading from carcasses. We used the model of Dillon and Rigler (1975) to estimate 5–8 years as the time to reach a new steady-state P level following a change in P loading.

The third argument used by Rounsefell (1958) to "settle" the fertility hypothesis turns out to be moot. However, it needs to be reviewed here as it was also cited erroneously by Owen et al. (1962). Rounsefell argued that intra-specific competition for food was not important because of a linear relationship between numbers and biomass of smolts. (If juvenile growth were density-dependent because of lowered lake fertility, a non-linear relationship would have been observed.) Rounsefell (1958) calculated a maximum potential smolt production for Karluk, using data from Barnaby (1944) at 13 226 000 smolts. However, this number is inflated because the survival rates used to back calculate smolt numbers from adults (17.4% age 1., 25.7% age 2.) were low (Ricker 1962). If the recalculated marine survival for Karluk smolts of 27.4% for age 1. and 34.2% for age 2. are used, maximum smolt production occurs at 8 717 000 fish. A recent model (Koenings and Burkett 1987) would predict Karluk rearing limitation at a much higher 18 000 000 smolts. Thus, even for the years of highest smolt production and using either 8.7 or 13.2 million as the potential, the density of sockeye fry was well below lake carrying capacity, and a linear relationship between smolt number and biomass would be expected regardless of the lake fertility question.

We conclude that the decline of the Karluk sockeye was not caused by a reduction in lake fertility, but the former certainly exacerbated the latter. It is now this latter decline in lake fertility that is the major stumbling block to restoration of sockeye production.

SMOLT PRODUCTION AND THE REARING ENVIRONMENT

During the time that adult production from Karluk Lake was routinely monitored, smolt production was also estimated in three non-contiguous studies (Fig. 1). Since low lake fertility is usually reflected in the small size and inferior growth

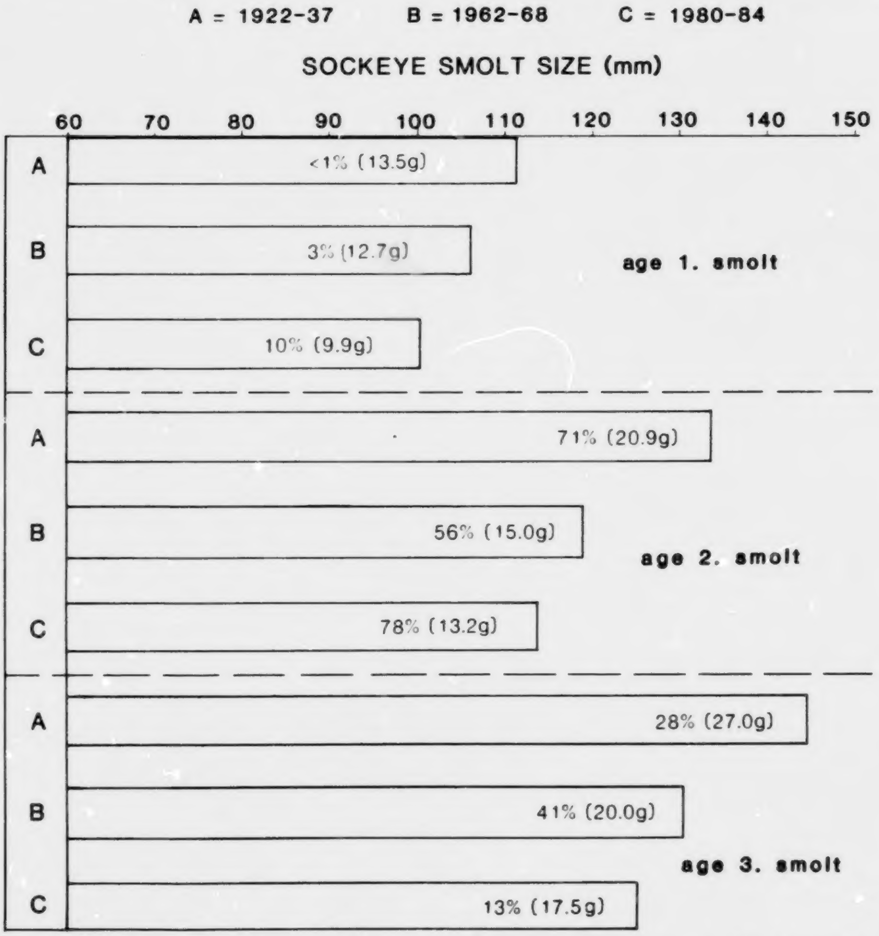

FIG. 7. The changes in length (mm) and weight (g) of three age classes (percent) of sockeye smolt from Karluk Lake during 1922–37 (A), 1962–68 (B), and 1980–84 (C). Smolt size and biomass estimates are weighted arithmetic means calculated from Barnaby (1944) and Rounsefell (1958), Drucker (1970), and White (1987), respectively.

patterns of resident fish (Owen et al. 1962; Koenings and Burkett 1987), we sought confirmation of fertility changes by comparing the size, age, and biomass of smolts (Fig. 7 and 8). This revealed substantial changes even though the first smolt study was conducted while the run was declining. Smolt production dropped from a mean of 5.8 million during the 1920's and 1930's to 1.83 million in the 1960's, and 1.25 million in the 1980's. Thus, like the decline in adult returns (Fig. 1), most of the smolt decline had occurred before 1960. A drop in the total biomass also occurred (Fig. 8) from 128 993 kg in the 1920's and 1930's, to 31 146 kg in the 1960's, and to only 17 902 kg in the 1980's. However, the ratio of weight to numbers was not constant, indicating that the average weight of the smolts dropped as well. Thus, in the 1920's and 1930's, the weighted mean smolt size was 22.2 g compared to 16.9 g in the 1960's and 13.4 g in the 1980's. If the fertility of the lake had remained constant, one would predict a lower number of juveniles and an increase in mean smolt size - not a decrease (Johnson 1965; Koenings and Burkett 1987). In fact, we found significant ($p < .01$; *f*-test) decreases between all three smolt age classes (Fig. 7) and that the greatest part of the decrease occurred between the 1920's and 1930's, and the 1960's, concomitant with the reduction in numbers of both adults (Fig. 1) and smolts (Fig. 8). From the period of the 1920's to the 1980's smolt numbers decreased by nearly 80%, weights decreased by 40%, and overall biomass decreased by nearly 90% (Fig. 8).

However, the age structure of smolts within each of these periods remained relatively stable (Fig. 7). Thus, the smolt age structure response to decreased densities of fry (as indicated by smolt numbers) appears to be, for the whole population, density-independent (see also Koenings and Burkett 1987). A density-dependent response should have resulted in larger fry and younger smolts (Johnson 1965; Koenings and Burkett 1987). We found little evidence in the smolt populations of either response (Fig. 7) indicating that as adult numbers and smolt numbers decreased, lake fertility had to decrease as well.

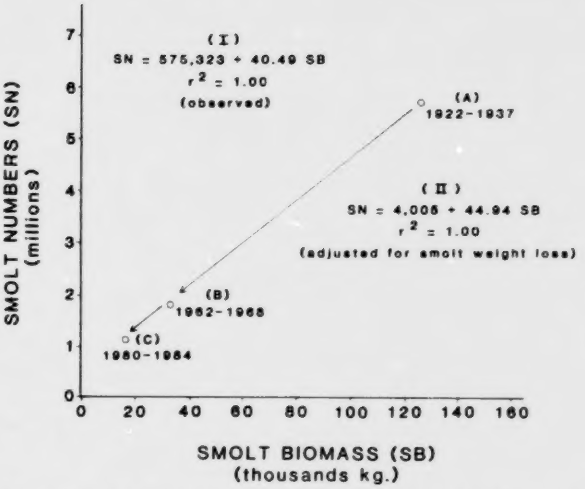

FIG. 8. The relationship between sockeye smolt abundance and biomass for Karluk Lake during 1922-37 (Barnaby 1944), 1962-68 (Drucker 1970), and 1980-84 (White 1987). The regression intercept of equation I (plotted) is high compared to the intercept of equation II because of a reduction in the weight of individual smolts from 1922-37 to 1980-84.

Still, one of the outstanding features of Karluk sockeye is their long period of lake residence relative to smolt size. Juveniles remain in the lake through size ranges at which those in other systems migrate (Owen et al. 1962; Hyatt and Stockner 1985; Koenings et al. 1985a; Koenings and Burkett 1987). Some investigators thought that by finding and alleviating the factors causing this delayed smolting, freshwater mortality could be reduced (Barnaby 1944; Rounsefell 1958; Owen et al. 1962), producing a corresponding increase in the adult runs. However, we feel that the cause of prolonged freshwater residence is neither inadequate nutrition (Barnaby 1944) nor superior growing conditions (Rounsefell 1958), but is related to the timing of zooplankton production and temperatures for juvenile rearing.

Rounsefell (1958) used Karluk as an example of an optimal rearing environment, as defined by summer surface temperatures between 8.8°C and 13.3°C. He felt that a favorable growth environment still existed between 7.2°C and 20.0°C, but below 7.2°C and above 20.0°C growth con-

TABLE 3. Comparison of thermal regimes at the surface and at 20 m in 1984 (warm) and 1985 (cold) within the three major Karluk Lake basins. Thermal regimes for juvenile growth are ranked according to Rounsefell (1958) from optimum (++) at ≥8.8°C to ≤13.3°C, favorable (+) at ≥7.2°C to ≥20°C, and unfavorable (−) at <7.2°C or >20°C.

			Heating period				Cooling period			
Lake (station)	Rearing year	Depth (m)	Start (date)	Mean temperature (°C)	Rank	End (date)	Start (date)	Mean temperature (°C)	Rank	End (date)
Karluk (2)	1984	1 m	04/10	11.5	++	08/17	08/18	11.9	++	10/20
		20 m	04/22	7.1	−	08/17	08/18	9.7	++	10/20
	1985	1 m	05/14	8.0	+	07/31	08/01	9.2	++	11/03
		20 m	05/27	5.2	−	07/31	08/01	7.3	+	11/03
Karluk (3)	1984	1 m	04/12	10.7	++	08/13	08/14	12.4	++	11/12
		20 m	04/17	5.7	−	08/13	08/14	7.3	+	11/12
	1985	1 m	05/12	6.1	−	07/25	07/26	9.2	++	10/14
		20 m	05/20	4.9	−	07/25	07/26	5.6	−	10/10
Karluk (4)	1984	1 m	04/11	11.3	++	08/12	08/13	12.6	++	11/04
		20 m	05/01	5.7	−	08/12	08/13	6.8	−	11/04
	1985	1 m	06/10	8.9	++	07/23	07/24	9.5	++	11/04
		20 m	06/10	6.7	−	07/23	07/24	7.2	+	11/04

ditions were unfavorable. In one warmer than usual (1984) and one colder than usual (1985) growing season during our recent study, surface temperatures were on this basis unfavourable in only one out of 12 measurements and optimal temperatures were recorded 10 out of 12 times (Table 3). Assuming that the juveniles rear largely at or near the surface, Karluk would still provide Rounsefell's (1958) optimal range of surface temperatures for juvenile growth during both the spring and fall periods. However, as surmised by Foerster (1968), Koenings et al. (1986) found that Karluk fry actually rear in the much cooler temperatures at or near 20 m. At such depths they were under an optimal thermal regime only once, and under totally unfavorable thermal conditions on a majority of occasions. Instead of peak food conversion efficiencies calculated by Rounsefell (1958), actual food conversion would be much less efficient, thus effectively slowing growth. Moreover, spring thermal regimes were much harsher than in the autumn. During the spring-summer rearing period conditions were unfavorable (6 of 6 times) at all stations in both years. In contrast, during the summer-fall period growing conditions reached optimum once, ranged between favorable and unfavorable on three out of six occasions, and were unfavorable only twice. Thus, the prolonged lake residence of Karluk juveniles appears to be a complicated, yet predictable, response to spring-fall temperature regimes within the lake.

The coupling of juvenile growth rates to rearing temperatures is very important, but so also is the linkage between growth, and both the timing and magnitude of forage production. For example, by fitting assumed food satiation, rearing temperatures at 20 m, and rearing time at Karluk to a sockeye growth model (Iwama and Tautz 1981), we still found predicted juvenile sizes after only one season to consistently exceed an estimated 2 g threshold-size for smolting (Koenings and Burkett 1987) (Table 4). This comparison indicates the potential influence of yearly variations in rearing temperatures on juvenile growth, and, since few smolts of age 1. are observed at Karluk (Fig. 7), it apparently invalidates the assumption of food satiated rearing used in the model. Growth rates of fry which enter the lake in early spring are retarded by lack of forage (Fig. 3) while the growth of fry entering later is limited by the shortened growing season (Table 3). Thus, we speculate that tremendous mortality may occur during the first year of lake residence due to negligible growth related to both the timing of forage production and to low rearing temperatures. We discount the notion of predation by arctic char (*Salvelinus alpinus*) as

TABLE 4. Body-weight comparisons between juvenile sockeye after one season's rearing in Karluk Lake at the surface (as suggested by Rounsefell 1958) or at 20 m (Koenings et al. 1986) using the growth model in Iwama and Tautz (1981); assuming food satiation, and using both the rearing period and rearing temperatures found at Station 3 in 1984 and 1985 (see Table 3).

	Rearing depth			
	Surface (1 m)		Deep (20 m)	
Spawning unit progeny	1984	1985	1984	1985
Spring run	27.7 g	5.8 g	7.2 g	3.1 g
Fall run	19.2 g	3.9 g	5.3 g	2.2 g

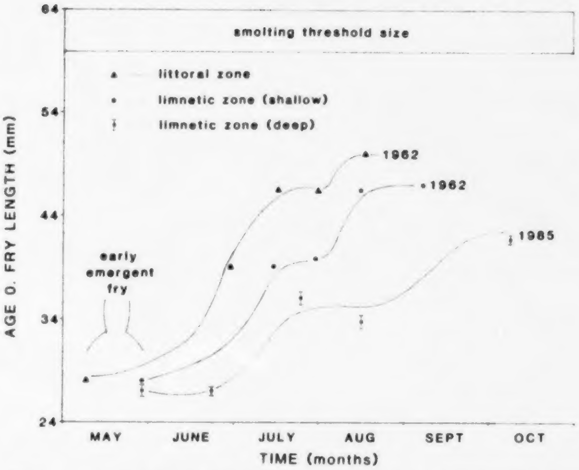

FIG. 9. Seasonal trends in sizes of age 0. Karluk juvenile sockeye trapped from the littoral zone, the shallow (surface) limnetic areas in 1962 (Gard and Drucker 1963), and deeper (18–20 m) limnetic strata in 1985. The early period of fry emergence is shown with the lag in apparent growth during July–August corresponding to the capture of smaller, later emerging fry. Individual points represent mean weights (1962) and mean weights ± 1 SE (1985).

determined by Rounsefell (1958). Because of slow fry growth (Fig. 9) smolt production is low, and age 2. and 3. smolts dominate (Fig. 7). These age groups at Karluk correspond to the age 1. and 2. smolts of most other sockeye systems. The lack of evidence for a gradual shift in age structure throughout the period of run decline (Fig. 7) is consistent with this hypothesis. Moreover, year-to-year shifts in estimated age structure can be explained by changes in rearing temperatures, freshwater survival, and/or relative escapements among the various stocks; and none of these is correlated with the continuing decline of the run. Thus, restoration of the run cannot be achieved solely by manipulating the age of seaward migration as suggested by Owen et al. (1962).

Despite efforts to increase escapements over the past 65 years, there has been no increase in smolt production (Fig. 8). Attempts to reverse the decline of the run have sought recruitment of more favorably timed fry by manipulating numbers in different spawning segments. However, Burgner et al. (1969) found that smolt production at Karluk fluctuated independently of the numbers in the parent escapements. Thus, for the run to recover, there must also be increased freshwater survival, since there is evidence that survival of Karluk sockeye smolts in the ocean has not declined (Drucker 1970; Koenings and Burkett 1987). Krogius (1961) emphasized that to obtain a high abundance of sockeye stocks it is necessary to maintain and increase the number of smolts because they are the primary determinant of abundance in the adult phase. Quite clearly, at Karluk Lake, a declining trend in smolt production has occurred (Fig. 8).

Conclusions and Recommendations

FRESHWATER THRUST AND PARRY: FRY RECRUITMENT AND SURVIVAL

Our approach to increasing the size of sockeye runs recognizes both the cause of the historical decline and, more importantly, the mechanism by which overfishing operated to modify several stock recruitment relationships resulting in lower productive capacity. We hypothesize that this mechanism operates in fresh water and has impeded management efforts to enhance smolt production. The key elements are the existence of several stocks spawning at different times and possessing characteristic freshwater age groups, the synchrony of their fry recruitment with forage production in the lake, and the duration of the rearing period.

Although their relative abundance varies annually, three to four age-groups comprise 90–95% of what remains of the original numerous groups (Table 5) and these can be represented as mid-season (age 2.2), spring (age 2.3), and fall (age 3.2) spawners (Fig. 2). The temporally separated spring and fall spawners may be genetically separate stocks that occupy different spawning habitats. In turn, spring spawners produce fry which migrate earlier than fry produced by fall spawners (Gard and Drucker 1965; Hartman et al. 1967; DiCostanzo 1972). Historically, however, fry could have been recruited throughout the season from overlapping spawning segments (Fig. 2) producing up to 20 freshwater/ocean age groups (Barnaby 1944). Thompson (1959) recognized that this mixture of age classes provided great flexibility and resilience for maintaining production under changing conditions.

The timing and number of fish caught and processed by local canneries was used to construct a seasonal distribution for the Karluk run (Rounsefell 1958). This resulted in hindcasting a historical (pre-1920's) single, mid-season peak even though the actual origins and species of the fish canned were never documented. Furthermore, the location of the adult weir may have confused the distinction between the timing of the spring and fall runs. During 1921–40, the weir was located near salt-water at Karluk Lagoon; however, from 1946–1975 it was located nearly 50 km upstream near the outlet of Karluk Lake. Consequently, early studies showing a mid-season low in escapements with an overlap between the two runs, contrasted with later studies where the runs were more distinct. Over time the question arose: What happened to the mid-season fish?

Presently, the major segments of the run still exist in proportions similar to 1922–37 (Table 5). That is, all segments of the run are numerically depressed. The mid-season spawners would have, presumably, produced fry entering the lake throughout the rearing period. That is, fry produced from both segments of the mid-period spawners (2.2) may have entered the lake during a period intermediate between that of fry from spring and fall spawners and would have produced both early and late migrating fry thereby balancing a synchronized forage production and fry entry schedule with duration of rearing. Thus, the life history strategy of a bimodal spawning distribution that has existed throughout the recorded history of Karluk sockeye production. Historically, the mid-season spawners may simply have been more numerous as the lake environment was more fertile and capable of supporting more juveniles.

Total annual production of zooplankton can be a misleading index of the availability of forage for fry, since production that occurs long before or after the fry inhabit the lake cannot be utilized. At present, fry growth in the lake is anemic, especially for the shallow and deep rearing groups of limnetic fry (Fig. 9). As a result, by the end of the first rearing year, very few fry have attained sufficient size to smoltify (Table 4). This retarded growth in any early period may be coupled to delayed peaks in zooplankton abundance (Fig. 3), which, in turn, may result in lowered freshwater survival rates (Johnson 1965; Koenings and Burkett 1987) and extended freshwater residence (Fig. 7). On the other hand, a late entry into the rearing area has costs associated with the shortened growing season. For example, DiConstanzo (1972) noted that scale patterns of the fall spawning 2.3 fish show the first freshwater annulus to be crowding the focus, indicating that they entered the first winter at a very small size. Because of this the progeny of the fall spawners remain in fresh water an extra year. The optimal time of fry entry resulting from the trade-off between the timing of peak forage production and the duration of rearing would probably lie between the spring and fall extremes. Thus, we would expect a positive correlation between total adult return (TR) and relative abundance of the combined age 2.2 subgroups (Fig. 2). In fact, there is a significant ($p<0.005$, t-test)

TABLE 5. Summary of age composition of sockeye escapements at Karluk Lake during 1922–37 (Barnaby 1944), 1962–68 (Drucker 1970), 1980–84 (White 1987), and in 1985. Age classes not listed comprised less than 10% of escapements, on average. Also shown are combined freshwater and ocean age-groups and the age composition of smolt samples (parentheses) taken during the same time intervals.

	Major adult ages in escapement (%)				Freshwater age (%)		Ocean age (%)	
Period	2.2 (5_3)	2.3 (6_3)	3.2 (6_4)	3.3 (7_4)	2.	3.	.2	.3
1922–37	55.3	15.7	20.0	1.6	71.0 (71.0)	21.6 (28.0)	75.3	17.3
1962–68	47.0	11.8	30.8	5.9	58.8 (56.0)	36.7 (41.0)	77.8	17.7
1980–84	52.4	26.7	7.4	2.1	79.1 (78.0)	9.5 (13.0)	59.8	28.8
1985	63.0	7.8	15.0	1.1	70.8	16.1	85.0	8.9

positive correlation ($\lvert \log TR\ (\text{thousands}) = 2.805 + 0.0075\ (\%2.2)\rvert\ r = 0.70$) for a period of 25 years from 1922 to 1948 (Barnaby 1944; Rounsefell 1958). The increased percentage of 2. fish from larger broods accounts for Rounsefell's (1958) observation that larger broods spend relatively less time in the lake, yet discounts his explanation that smaller broods had better rearing conditions and thus stayed longer in the lake.

We have measured Karluk lake zooplankton density since 1979 (Fig. 10) and the seasonal pattern has been consistent (Fig. 3). Thus, while an annual increase in total numbers of forage items could be beneficial for all fry, the time of maximum density may consistently favor those fry entering later in the season. In our view, the spring spawners would be less productive (e.g., lower return/spawner) than the later spawners. This view is consistent with return per spawner differences in the 1985 escapement in that the return per spawner equalled <2: 1 for the early spawners versus 19: 1 for the late run. High forage density during 1981 and 1982 (Fig. 10) appears to have enhanced production of both age 2. and 3. smolts in 1983 since these smolts produced a 25-yr-high escapement of nearly one million adults in 1985. This run was particularly strong both in the age 2.2 middle segment and the age 3.2 fall-spawning segment (Table 5). Moreover, zooplankton production at Karluk peaked in 1983, so smolt production should be high in 1984 and produce even higher returns in 1986.

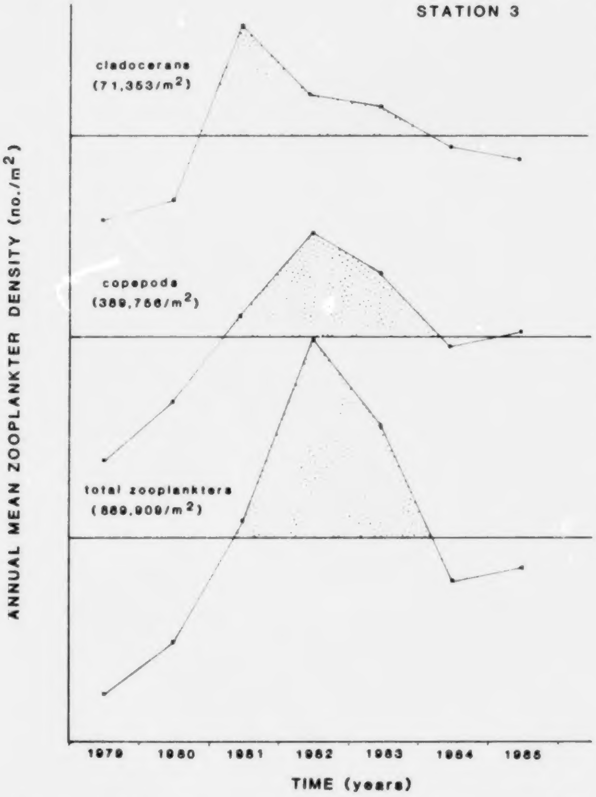

FIG. 10. The change in mean (May–October) macrozooplankter density over the 1979–85 period at station 3 in Karluk Lake. The 7-yr arithmetic mean (given) is represented by the horizontal line within each category; individual points represent the actual estimates.

THE SOLUTION

We offer two approaches, aimed at increasing both juvenile recruitment and survival, to restore the Karluk sockeye. First, we feel the evidence foretells increased fry-to-smolt survival as a result of excellent rearing conditions in 1981 and 1982 (the corresponding adult return in 1985 has already set a modern record). Unfortunately, the production of zooplankters has recently begun to decline (Fig. 10) and, consequently, a higher than average fry recruitment may now be forced to exploit a lower than average forage base. Indeed, juvenile growth in 1985 was poor (Fig. 9) with age 0. fry reaching a mean size of only 42 mm by October. As lake nutrient levels are extremely variable (Fig. 4) and are not tied directly to fish carcass P (Fig. 6), we recommend fertilizing the Main basin of the lake (Table 1) with nitrogen and phosphorus (see Hyatt and Stockner 1985; Koenings and Burkett 1987 for discussion of treatments) to enhance the forage for expected increases in fry recruitment in 1986 and 1987. Synchrony of Karluk Lake forage production and fry emergence can be achieved by judicious application of nutrients. Enrichment should be timed to enhance the forage supply during the critical spring period (Barraclough and Robinson 1972), when fry first enter the lake.

Second, prior researchers have recommended manipulations of escapements to affect both a greater number and a more advantageous recruitment of fry (Fig. 11). However, the previously unknown in-lake fertility problems, which adversely affected fry survival, largely prevented such manipulations from reversing the decline of the runs (Fig. 1).

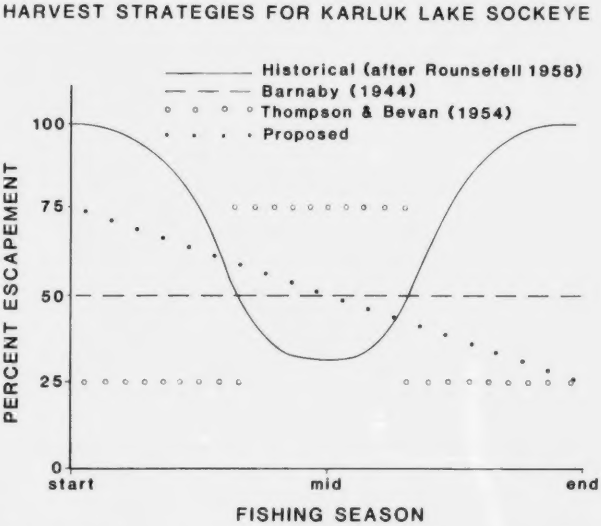

FIG. 11. Comparison of harvest strategies based on escapement timing for historical observations with a mid-season emphasis (Rounsefell 1958; Owen et al. 1962), the constant proportion approach (Barnaby 1944), the mid-season protection proposal (Thompson and Bevan 1954), and the sliding scale proposed here for the Karluk sockeye run.

The proposed fertilization is designed to increase the survival of fry from each spawner segment, yet the harsher rearing environment (Table 3) in the spring argues a greater benefit for later emerging fry, i.e., from both the mid-season and fall spawners. As the intent is to enhance all stocks within the overall run (Table 5), the spring run requires a larger number of spawners to compensate for the survival disadvantages of early emergence. For this reason, we support the continuance of the Upper Thumb River supplemental production project that seeks to increase recruits from the spring run through eyed egg plants. As this is only a subcomponent of the spring run, we would also alter harvest strategies to balance stock specific increases in numbers of recruits with the increased survivals of others. For this to occur, we would stress a strategy of steadily increasing the harvest (decreasing escapements) throughout the season instead of the historic mid-season emphasis described by both Rounsefell (1958) and Owen et al. (1962), the opposing strategy of Thompson and Bevan (1954), and the constant proportion approach of Barnaby (1944) (Fig. 11). Combining the manipulation of both escapements and lake fertility may well align smolt production of each spawner segment to escapements, a long sought after goal at Karluk (Barnaby 1944; Rounsefell 1958; Owen et al. 1962; Burgner et al. 1969; Drucker 1970; and Van Cleve and Bevan 1973).

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Barkley Sound Sockeye Salmon (*Oncorhynchus nerka*): Evidence for over a Century of Successful Stock Development, Fisheries Management, Research, and Enhancement Effort

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Abstract

HYATT, K. D., AND G. J. STEER. 1987. Barkley Sound sockeye salmon (*Oncorhynchus nerka*): evidence for over a century of successful stock development, fisheries management, research, and enhancement effort, p. 435-457. *In* H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Approximately 100 years of variations in the catches of three stocks of sockeye salmon (*Oncorhynchus nerka*) returning to Barkley Sound on the west coast of Vancouver Island are examined to determine the effects of harvesting and habitat alteration as well as management, stock development, and research activities by Canada's Department of Fisheries and Oceans and its predecessors. The fishery has passed through several phases including: largely terminal subsistence fishery that probably harvested no more than 50 000 sockeye per year (pre-1900), a terminal beach-seine and gillnet fishery that provided catches as high as 125 000 sockeye (1900–40), a more diffuse gillnet fishery that exploited mixtures of sockeye in Alberni Inlet and the outer waters of Barkley Sound yielding catches of 5 000 to 76 000 sockeye (1940–71), and finally a mixed gear, mixed stock fishery in which gillnetters and purse-seiners harvested between 150 000 and 1 200 000 sockeye per annum (1972–85). Habitat protection measures have on at least three occasions prevented the almost certain destruction of one or more of the Barkley Sound sockeye stocks. Gear and area restrictions within the commercial fishery have been used with varying effectiveness throughout the past century to focus exploitation rates or stock rebuilding efforts alternately on Henderson Lake or Somass River sockeye stocks. Stock development and enhancement activities have included: removal of obstructions to fish passage (1901, 1903, 1912–16, 1936); construction and maintenance of fishways at Stamp Falls (1927, 1954), Sproat Falls (1951), and the outlet of Great Central Lake (1929, 1957); operation of a sockeye hatchery on Henderson Lake (1909–35); planting of eyed eggs and sockeye fry from the Henderson Lake hatchery into Sproat and Great Central Lakes (1921–32); fertilization of Great Central Lake (1970–73, 1977–85), Henderson Lake (1976–85), and Sproat Lake (1985); and escapement optimization (1972–85). Recently, lake fertilization, in combination with escapement optimization, has been used to increase the production of Barkley Sound sockeye to historically unprecedented levels and has made them the focus of a major commercial fishery. However, it is doubtful that this would have been achieved in the absence of the other stock protection and enhancement activities that have contributed over the past century to either the maintenance or development of the Barkley Sound stocks.

Résumé

HYATT, K. D., AND G. J. STEER. 1987. Barkley Sound sockeye salmon (*Oncorhynchus nerka*): evidence for over a century of successful stock development, fisheries management, research, and enhancement effort, p. 435-457. *In* H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Les auteurs examinent des données, recueillies pendant environ 100 ans, sur les prises pour trois stocks de saumon nerka (*Oncorhynchus nerka*) amontant dans la baie Barkley, sur la côte ouest de l'île de Vancouver, afin de déterminer l'incidence de l'exploitation et de la dégradation de l'habitat ainsi que des activités de gestion, de mise en valeur des stocks et de recherche effectuées par le ministère canadien des Pêches et des Océans et ses prédécesseurs. La pêche a passé par plusieurs phases dont une pêche de subsistance en estuaire où probablement 50 000 saumons nerkas au plus étaient capturés annuellement (avant 1900), une pêche en estuaire à la senne de rivage et aux filets maillants qui a généré des prises allant jusqu'à 125 000 saumons nerkas (1900–1940), une pêche moins concentrée aux filets maillants qui exploitait des stocks mixtes de saumons nerkas de l'inlet Alberni et des eaux extérieures de la baie Barkley (1940–1971 : de 5 000 à 76 000 saumons nerkas) et finalement une pêche pluristocks à l'aide de divers engins où les bateaux de pêche aux filets maillants et les senneurs ont capturé de 150 000 à 1 200 000 saumons nerkas annuellement (1972–1985). Les mesures de protection de l'habitat ont empêché, au moins à trois occasions, la destruction presque certaine d'un ou plusieurs stocks de saumon nerka de la baie Barkley. Des limites par secteur et par engin pour la pêche commerciale ont été utilisées avec divers degrés d'efficacité au cours des cent dernières années pour concentrer les taux d'exploitation ou les efforts de remise en valeur alternativement sur les stocks de saumon nerka du lac Henderson et ceux de la rivière Somass. Parmi les activités de repeuplement et de mise en valeur des stocks, on retrouve les suivantes : l'enlèvement des obstacles au passage du poisson (1901, 1903, 1912–1916, 1936); la construction et l'entretien d'échelles à poissons aux chutes Stamp (1927, 1954), aux chutes Sproat (1951) et à l'émissaire du lac Great Central (1929, 1957); l'exploitation d'une écloserie de saumon nerka au lac Henderson (1909–1935); le déversement d'oeufs embryonnés et d'alevins de saumon nerka provenant de l'écloserie du lac Henderson dans le lac Sproat et le lac Great Central (1921–1932); la fertilisation du lac Great Central (1970–1973, 1977–1985), du lac Henderson (1976–1985) et du lac Sproat (1985); et l'optimisation de l'échappée pour accroître la production de saumon nerka dans la baie Barkley, qui a atteint des niveaux encore jamais vus et et fait l'objet d'une importante pêche commerciale. Toutefois, il est peu probable que ceci aurait pu être réalisé en l'absence d'autres activités de protection et de mise en valeur des stocks qui ont contribué, au cours de ces cent dernières années, à la survie ou au développement des stocks de la baie Barkley.

Introduction

Reuben Ware (1983), in a recent text summarizing the historical development of relations between the Department of Fisheries and native Indians in British Columbia, provides an unflattering view of the Department's success in developing and protecting the salmon resource over the past 100 years. He states "It has been the direct responsibility of the Federal Fisheries Department to protect salmon spawning areas and the salmon resource" but that "while they were confiscating a few nets, smashing weirs, and harassing Indians practicing their aboriginal rights, the resource was being severely depleted." He then poses a commonly uttered rhetorical question "Where was the Fisheries Department when the ecological damage to the Salmon was being done?"

The answer to this question with respect to stocks of sockeye salmon in many locations seems self evident as histories of sockeye stock declines on the Columbia (Mullan 1984), the Fraser (Williams 1987), Rivers Inlet, and other locations such as Karluk Lake in Alaska (Gard et al. 1987), and the Ozernaya River of Kamchatka (Selifinov, 1987) suggest that Fisheries Departments have either been distracted or overwhelmed by impacts of commercial fisheries and other resource development activities on salmon to the point where the declines of many stocks were inevitable. There are, however, exceptions where development, management, and research activities appear to have achieved remarkable success in spite of the odds against it. In this paper, we document one of these exceptions as testimony to more than a century of successful effort and problem solving by Canada's Department of Fisheries and Oceans and its predecessors to develop and effectively manage habitat and fisheries associated with three sockeye stocks returning to Barkley Sound on the west coast of Vancouver Island. In what follows, we present evidence for what we believe have been the critical development, management, and research interactions that have promoted this success.

Methods and Data Sources

Study Area and History

The Barkley Sound study area is located on the west coast of Vancouver Island and has been described in detail in various publications both technical (Manzer 1976) and popular (Scott 1972). The Somass River drainage has been undergoing intensive development for approximately 125 years. During this interval, timber has been cut, the commercial fisheries of Barkley Sound have been developed, mineral resources exploited, power projects planned and executed, river hydrology altered both for industrial and fish development purposes, urban population centers have developed, and secondary industries have become established (Sproat 1868; Carmichael 1908; Walbran 1909; Bird 1971; Hill 1952). In many ways development trends in the Alberni Valley and the watershed of the Somass River have "played out" in microcosm the story of settlement and development on a larger scale in the province of B. C. itself. All of these activities have had the potential to greatly influence the fate of the anadromous stocks of salmon returning to Alberni Inlet and the Somass River and indeed it is common to hear anecdotal accounts of how changes in one or more of these have altered the strength of the salmon stocks. However, anecdotes are a poor substitute for systematic review and analysis, and consequently one of the goals of this paper is to compile a general record of resource development activities and associated changes in the sockeye stocks, which are the most abundant stocks of salmon returning to the Barkley Sound, Somass River area. It is hoped that this review will provide additional insight into events that have had a profound effect on the sockeye as well as changes that have played a less important role.

Sources of Observations and Data

This paper is developed in two major steps. The first involves quantification of changes in the total stock size of sockeye salmon returning to Barkley Sound and Alberni Inlet over the period of record. The second step involves relating these changes, in order of presentation to: (i) general developmental patterns in the coastwide salmon fisheries, (ii) specific developmental events in the Barkley Sound fishery, (iii) developmental patterns of fisheries regulation, (iv) habitat development and protection activities in the Barkley Sound and Alberni Inlet region, and (v) stock development initiatives undertaken with respect to the Barkley Sound sockeye stocks.

We have made extensive use of a number of key historical accounts to relate Barkley Sound sockeye stock variations to the various categories listed above. Chief among these have been historical texts by Lyons (1969) on the development of coastwide salmon fisheries, and by Walbran (1909), Hill (1952), and Bird (1971), on industrial development patterns characterizing various periods in the Barkley Sound, Alberni Inlet region. The numerical data have been largely collected from published papers, unpublished reports or data records of the Department of Fisheries and Oceans, and our own research on the Barkley Sound stocks. These sources of data are as follows:

1) Reports on stock performance and annual sockeye pack for Barkley Sound contained in Annual Reports of the Department of Fisheries (DF), the Department of Marine and Fisheries (DMF), and the Department of the Naval Service (DNS), 1884 to 1941.

2) Reports of the Commissioner of Fisheries for British Columbia, 1903–21.

3) Canada Department of Fisheries and Oceans (DFO) reports and records including:

(a) Annual Narrative Reports for the Barkley Sound subdistrict, 1927–68.
(b) Area History Reports, Area 23, 1951–82.
(c) Weekly Reports of Fisheries Officers, Area 23, 1947–82.
(d) Weekly Reports of Fisheries Guardians, Area 23, 1950–76.
(e) Annual Catch Statistics, 1950-present.
(f) Correspondence to File re: Propagation of fish, 1927–32, and obstructions to fish passage and fishways, 1925–60.
(g) Miscellaneous correspondence in files of various branches of the Department.

Information on the magnitude of sockeye returns by stock, the development and implementation of fishery regulations, habitat protection activities, sockeye stock conservation events, and stock development initiatives were transcribed from unpublished sources, in as much detail as possible. Wherever available, the following information was recorded by year: (i) catch by stock, (ii) escapement by stock, (iii) openings and closures of the sockeye fishery by time and statistical subarea, (iv) gear regulations, (v) fishing vessel numbers, (vi) fishing vessel type, and (vii) sockeye passage success by date at key points in the Somass River system. Key items from these records are presented in this report. Methods associated with data from other studies will be referenced along with their sources where appropriate.

Results and Discussion

Due to the long time series of observations to be presented here and the requirement to relate stock fluctuations to various events that were temporally proximal, we have presented the results and discussion in six time periods, i.e., >4000 B.P. – late 1800's, 1860–1900, 1901–20, 1921–40, 1941–60, and 1961–83. In general, each section begins with a brief overview and then in sequence deals with (i) a brief description of pertinent key developments in the coastwide salmon fisheries, (ii) specific developmental events in the Barkley Sound sockeye fishery, (iii) developmental patterns of fisheries regulation, (iv) habitat development and protection activities in the Barkley Sound and Alberni Inlet region, and (v) stock development initiatives undertaken with respect to the Barkley Sound sockeye stocks. Finally, catch and escapment patterns within each time period are presented and discussed within the context of these other events.

>4000 B.P. – late 1800's

During this time period, Native subsistence fisheries concentrated at the mouths and along the lower reaches of the Henderson[1], Somass, and Sproat rivers (Fig. 1). Fish were utilized by an aboriginal population numbering no more than 1000–2000 individuals which may have generated a demand for a maximum of 30 000 to 100 000 sockeye per year (Hyatt and Winters, unpublished MS, Pacific Biological Station, Nanaimo, B.C.). Sockeye harvest was obtained through a combination of spearfishing from canoes and deployment of traps or weirs along specific river reaches (Drucker 1951). Consideration of fishing techniques, gear efficiency, and annual run duration suggests that the capacity existed to harvest sufficient numbers of sockeye to meet this demand.

1860–1900

OVERVIEW

This was a transitional period during which (i) Native food fisheries accomodated to the effects of non-Native settlement and development activities in Barkley Sound and Alberni Inlet, (ii) first initiatives were taken to develop the commercial sockeye fishery, (iii) the Dominion Government instituted policies to control the harvest and processing of salmon, and (iv) non-fishery resource development activities began to pose serious threats to salmon stocks.

FISHERY DEVELOPMENT 1860–1900

The settlement of Alberni was established in 1860 with a non-Native population of 40 at the head of Alberni Inlet (Nicholson 1962). By comparison, census indicated the Native population in 1860 consisted of 399 adult males (sources as per McMillan and St. Claire 1982) or roughly 1200 people. Non-Native settlement and development in the Alberni area altered both patterns of Native settlement and fishing. The site of the major Indian village on the lower Somass was relinquished in 1860 through a treaty with Captain Edward Stamp to make way for a lumber mill (Hill 1952). Traditional fishing sites at the base of Sproat Falls (Fig. 1) as well as along the lower Somass were utilized less frequently. Construction of Papermill Dam at the first rapids about 2 miles from the mouth of the Somass in 1893 (Bird 1971) focused Native food-fish harvesting and processing on this location (Fig. 1). Indian Agent H. Guillod (1898) reported that "since the papermill Dam was put across the river, about two miles from the mouth, all the salmon wanted by the Indians for their supply of dry fish food are taken by spear and net just below the dam." Bird (1971) noted that

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[1] The Henderson River (immediately below Henderson Lake) was frequently referred to in early reports and correspondence as the Anderson River. To avoid confusion, place names identified as Anderson River, Anderson Lake, and Anderson Lake hatchery have been identified throughout the text as Henderson River, Henderson Lake, and Henderson Lake hatchery.

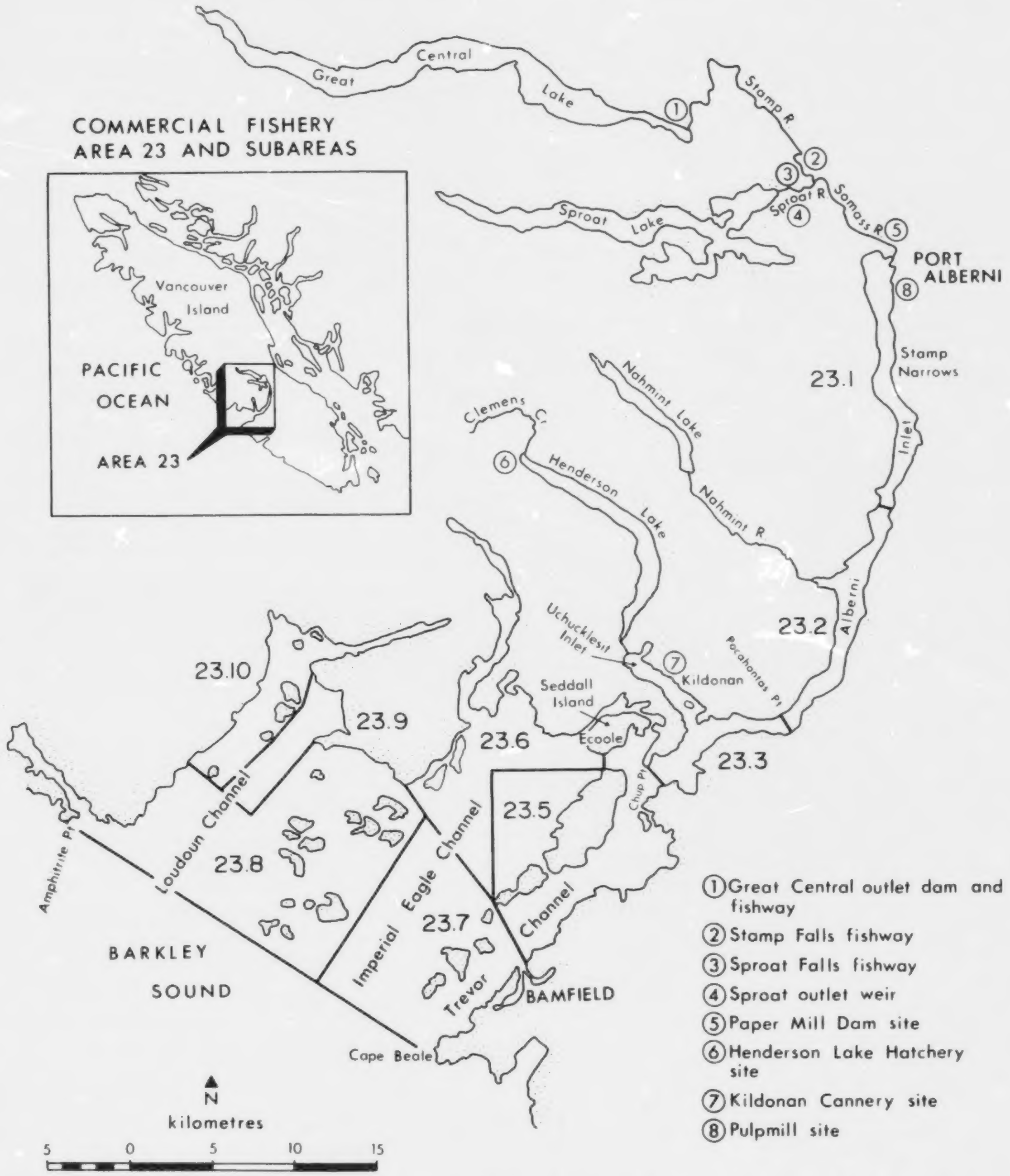
COMMERCIAL FISHERY AREA 23 AND SUBAREAS
Vancouver Island
PACIFIC OCEAN
AREA 23
Great Central Lake
Stamp R
Sproat Lake
Sproat R
Somass R
PORT ALBERNI
Stamp Narrows
Alberni Inlet
Nahmint Lake
Nahmint R
Clemens Cr
Henderson Lake
Uchucklesit Inlet
Kildonan
Pocahontas Pt
Seddall Island
Ecoole
Chup Pt
23.1
23.2
23.3
23.5
23.6
23.7
23.8
23.9
23.10
Loudoun Channel
Imperial Eagle Channel
Trevor Channel
Amphitrite Pt
BARKLEY SOUND
BAMFIELD
Cape Beale
N
kilometres
5
0
5
10
15
①Great Central outlet dam and fishway
②Stamp Falls fishway
③Sproat Falls fishway
④Sproat outlet weir
⑤Paper Mill Dam site
⑥Henderson Lake Hatchery site
⑦Kildonan Cannery site
⑧Pulpmill site

FIG. 1. The Barkley Sound, Alberni Inlet study area (Statistical Area 23). Cellular divisions numbered 23.1 to 23.10 indicate the ten statistical subareas in which openings and closures are used to control the fisheries for sockeye.

the Natives had several large houses there, where they cured their winter supply of fish. Sometimes there would be a half dozen or more canoes. The canoemen threw the salmon in huge heaps on the grassy bank where the old women cleaned them, then placed them on racks in the upper part of the building to smoke. In 1890 at Uchucklesit Inlet, the harbour was developed as a settlement and port, but it is unlikely that this disrupted Native fishing patterns at the mouth of the Henderson River to any great extent.

Evidence for commercialization of the salmon fishery in general and the sockeye catch in particular, indicates participation by both Native and non-Native groups. Bird (1971) reported that the town of Alberni had no fish or meat markets during this period. However, the Indians were permitted to catch salmon for sale. A fishing station was operated in Barkley Sound as early as 1860 by Edward Stamp (Bird 1971). The sale and export of mild-cured, salted sockeye processed on the lower Somass had begun by 1893. However, the demand may not have been very great as poor market conditions prevailed in the late 1800's due to a glut of salmon on the British market which in turn dampened innovation and the rapid development of sockeye fisheries as capital sources dried up (Stacey 1982). In support of this, Bird reports observing (circa 1893) a warehouse on the lower Somass containing at least 100 barrels of salted sockeye in a state of "decay" owing to the lack of a market. By 1857, the Barclay [sic] Sound Fishing Company was taking a commercial catch of salmon under regulations set by Federal fisheries (Ann. Rep. DMF 1887). Salmon may have been harvested under an exclusive license arrangement (see details in Lyons 1969).

The small local population base in the Barkley Sound-Alberni Inlet region, as well as the depressed condition of any potential export markets, did not promote rapid change in the sockeye fishery during this interval. Little, if any, mechanization of harvesting or processing techniques had been introduced. Native fishermen likely still obtained most of the sockeye catch by traditional methods (spearing from canoes, deployment of traps and weirs) in terminal locations at the mouths of the rivers, although some decline in the use of traditional trap-sites may have occurred. Commercial gear introduced by non-natives would have consisted of nets (drag seines, gillnets) and small, shallow-draft, oar, or sail driven vessels of the Columbia or Fraser River design (see Stacey 1972; Lyons 1969 for examples).

FISHERY REGULATION 1860–1900

Dominion Government salmon fishery regulations were not specific to Barkley Sound-Alberni Inlet, but were applied to all of British Columbia. Federal regulations first came into effect in 1875 through extension of the Fishery Act to British Columbia and appointment of the first B.C. Fishery Inspector (A.C. Anderson). The regulations were first applied to the Fraser River sockeye fishery in 1876 (Lyons 1969; Stacey 1982; Ware 1983). The effect of these regulations was to theoretically abolish all net salmon fishing in the fresh waters of B.C. Further, the regulations set the time of fishing to the period outside of 08:00 on Saturdays to midnight on Sundays.

HABITAT PROTECTION 1860–1900

The development of non-fishery resources inevitably posed threats to the salmon stocks, particularly in the Somass watershed. For example, logging operations lasted on Sproat Lake from 1861 to 1866. They were shut down in 1866 due to a lack of readily accessible timber (Hill 1952). Towards the end of this period G.M. Sproat, the mill manager, reported that more logs had been obtained by making a dam at the outlet of Sproat Lake enabling logs to be floated down the river to the mill. At that time, the only alternative way to convey logs to the mill was to drag them with oxen (Bird 1971). It is not known how long this Sproat Lake outlet dam remained in place; however, such a structure would undoubtedly have produced difficulty for passage of sockeye salmon up to their spawning grounds in Sproat Lake. Similarly, construction of the 4 m high Papermill Dam across the lower Somass created a formidable barrier preventing the ascent of all salmon species beyond the lower 4 km of the lower Somass between 1893 and 1895. A fish ladder had been incorporated into the dam "but it did not prove effective" (Ann. Rep. DMF 1902). The paper mill closed in 1895 due to a lack of raw materials; however, the dam was left in place in consideration of future ventures. This led Fisheries Overseer Guillod to observe in 1898 that "as a new company has formed to operate the mill this season, it is urgent that a proper and substantial fishway be built during the coming summer and one suitable to all species of salmon" (cited in Ware 1983). Apparently the mill did not reopen, thus, from 1895 to 1901 Federal fisheries personnel ensured that the dam's sluice gates were left open to permit sockeye salmon passage. In 1901 fisheries personnel removed the gates entirely. Although little commentary exists regarding the quantitative effects such events had on sockeye production in the Somass, it is likely that stocks returning to either Sproat or Great Central lakes by way of the lower Somass would have been decimated by the combination of increased vulnerability to terminal fisheries by native peoples at the base of the dam as well as by either total (1893–94) or partial loss (1895–1901) of access to their spawning grounds over an 8-yr period. Without the concerns and actions taken during this period by fisheries personnel it is doubtful that Somass sockeye stocks would have persisted.

SOCKEYE STOCK DEVELOPMENT 1860–1900

Few, if any, sockeye stock development initiatives were made during this period.

SOCKEYE CATCH 1860–1900

No catch statistics are available for this period, however, in addition to the demand for food-fish by the aboriginal population, some sockeye were sold or eaten by the non-Native population. For example, the barrels of salted sockeye observed by Bird were known as tierces. A full tierce weighed approximately 825 lb and required roughly 1000 lb of raw salmon to fill it (Forester and Forester 1975). Therefore, given an average fresh weight of roughly 5.64 lb for a Barkley Sound sockeye (K. Hyatt, unpublished data), the 100 tierces observed by Bird would have represented a minimum catch of 19 467 sockeye. Given the knowledge that poor market conditions would preclude selling even these quantities, it is likely that the local demand for food fish continued to set the upper limit on sockeye catch during the period from 1860 to 1900. Accordingly, the catch was probably still no more than the 30 000 to 100 000 sockeye noted above for the interval prior to 1860.

1901–20

OVERVIEW

This was a period of increasingly rapid development of the commercial fishery characterized by: (i) capitalization of new fish processing facilities, (ii) fishing fleet expansion and mechanization, (iii) intensive exploitation of sockeye in terminal rivermouth fisheries, (iv) increased conflict between Native and non-Native peoples over fishing activities on the Somass and in Alberni Inlet, and (v) a growing concern over the potential for sockeye salmon stock declines, and an increased frequency of intervention by Federal fisheries personnel to reduce both natural and man-induced habitat limitations on sockeye production.

FISHERY DEVELOPMENT 1901–20

The Alberni Valley exhibited sustained population growth during this period and by 1913, 1800 people lived in the villages of New Alberni and Port Alberni. Transportation links both within the region and to the outside were steadily improving. Sproat Lake and Great Central Lake were connected by road in 1905 (Hill 1952). In 1911, the E & N railway connected Port Alberni with the east side of Vancouver Island.

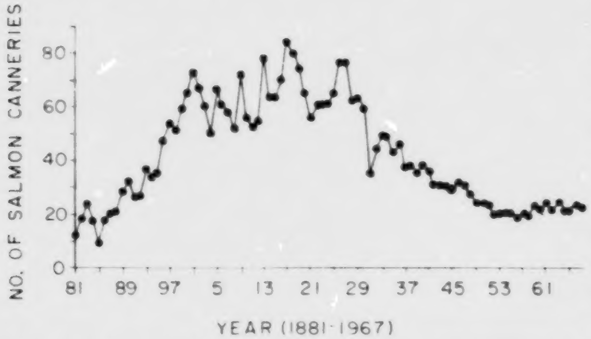

FIG. 2. Historical trends in the number of salmon canneries in operation on the British Columbia coast in each year from 1881 to 1967. Data principally from Appendix 36 of Lyons (1969).

By 1900, the number of salmon canneries and their output along the B.C. coast had expanded dramatically (Fig. 2), although this expansion was moderated by Federal regulations covering licensing of salmon cannery operations (Lyons 1969; Pearse 1982). Reid (1973) has documented the general trend for a consolidation of capital and organization of the salmon fishing and processing enterprise into fewer large holdings (e.g., British Columbia Packers was formed through consolidation of a number of smaller interests in 1902). This was also a period of active capital investment in new plant and fishing fleet capacity associated with the sockeye fishery of Barkley Sound and Alberni Inlet. The first narrows on Alberni Canal [sic] very nearly became the site of a fish trap as John Kendall, a pioneer in the fish business in Port Alberni, spent much money and effort to obtain a license for a trap in Barkley Sound. However, efforts to build a trap failed as the water was too deep to drive the necessary piles (Bird 1971). In 1903, the Alberni Packing Company built the Uchucklesit Cannery midway along the southeastern shore of Uchucklesit Inlet (Ann. Rep. DMF 1903; Paterson 1979). In 1909, the Alberni Packing Company was sold to Wallace Brothers and the Uchucklesit Cannery name changed to Kildonan (Paterson 1979). Fish handling capacity was increased through the addition of a cold storage plant at Kildonan in 1912 (Bird 1971).

Fishing fleet expansion and mechanization in both the fishing and fish processing sectors occurred rapidly. Drag seines and gillnets, deployed for the most part at the mouths of the Henderson and Somass rivers, had become the principal gear used to harvest sockeye returning to Barkley Sound. Wood (1922) observed the Henderson River from 1913 to 1918 when it was fished (for sockeye) by drag seine close to the mouth of the river, and in 1919 by purse seine only. "During all these years of intensive fishery the run was steady and uniform. The pack at Wallace Fisheries Cannery running [sic] from 1200 to 1500 cases (i.e. approximately 18 000–32 000 sockeye) each year." Indeed, the catch from the Henderson River terminal fishery apparently accounted for most of the commercial sockeye pack during these years.

In addition to fleet expansion, rapid technological change was occurring in the fishing and fish-transport sections of the salmon industry. Stacey (1982) documented rapid technological change between 1871 and 1912 in the canning, fishing, and tender sections of the Fraser River salmon industry. Evidence that a series of parallel changes were taking place in the Barkley Sound fleet is suggested by Bird (1971) who, in summarizing the state of the fishery in the Barkley Sound–Alberni Inlet region about 1910, said that "one after another, the Columbia or Fraser type of saiboats which had been used by the Indians disappeared, or had motors installed in them. White fishermen began to use gas boats, and trolling for salmon became general."

Mechanization of gillnetters produced distinct advantages over oar and sail powered vessels. It increased the fishing area by extending it offshore. It increased fishing time by reducing travel time and facilitated fishing in rough weather. Gasoline engines also made a purse seine fishery practical, and powered purse-seine winches, in use by 1907, reduced the time and labour required. Mechanized seines could make twice the number of daily sets that their non-mechanized counterparts could. Thus, effective fishing effort for Barkley Sound sockeye likely increased appreciably between 1903 and 1915.

The disposition of native Indians and their food-fishery deteriorated considerably during this period. Native concerns are indicated in a number of reports. For instance, in 1904, Barkley Sound Indians requested a hatchery to maintain the supply of fish which they feared would be adversely affected by the Alberni Packing Company (Ann. Rep. DMF 1904). Later, in 1914, testimony by Chief Dan Watts and Chief Shewish to the Royal Commission on Indian Affairs suggests increasing conflict between Native and non-Native people over fishing activities on the Somass. They complained of interference with the traditional operation of salmon traps on the river and of an expanding purse seine fishery (Appendix 10 of Ware 1983).

These concerns were shared by non-Natives, and appear to have peaked in 1919–20. In 1919, a judicial investigation by a Judge Eberts followed requests from the fishermen of Barkley Sound and the people of the Alberni area for an impartial investigation into the perceived destruction of herring and the depletion of local salmon stocks (Lyons 1969). Even the fish processors of the area seemed concerned as Mr. Wallace, the head of Wallace Fisheries at Kildonan, was quoted in a January 1920 article to the Daily Province newspaper as having said that "the [stock] situation is so serious that it will only be a question of two years when there will be no fish left" (Wood 1934).

FISHERY REGULATION 1901–20

Fisheries regulations during this period appear to have been similar to those implemented from 1860 to 1900. Prior to 1904, purse seines had been barred from operation in B. C. coastal salmon fisheries (Forester and Forester 1975), but they then gained entry to the fishery and the Henderson Lake sockeye stock was harvested principally by purse seine in Uchucklesit Inlet during 1919 (Wood 1922). There were few, if any, restrictions on the use of various gear types (gillnet, drag seines, purse seines) in the fishery. Given concerns over the depletion of salmon stocks in general, and the Henderson sockeye in particular, Uchucklesit Inlet and the Henderson River (Fig. 1) were closed by regulations to all fishing beginning in 1920 with the intent of increasing returns to the hatchery (see details below) and permitting the stock to recover.

HABITAT PROTECTION 1901–20

In 1915–16, a large portion of the old Papermill Dam was removed from the lower Somass. Although the sluice gates were removed in 1902 and rock was blasted away to ease fish passage, E. G. Taylor, the Inspector of Fisheries, wrote that stream flow through existing gaps (13 yr later) was such that salmon were often unable to ascend freely. "After inspection, it was decided to remove sufficient of the remaining portion of the dam to give an unobstructed width of between 75 and 80 feet to the river." After this work, the fishery guardian for the district reported that the salmon were able to ascend the river with very little difficulty into the spawning areas in Sproat Lake (Ann. Rep. DNS 1915–16).

SOCKEYE STOCK DEVELOPMENT 1901–20

By the early 1900's, fisheries personnel had identified hydraulic conditions at both Stamp and Sproat Falls (Fig. 1) as constituting a serious recurring problem for free passage of sockeye, as well as other salmon species, to their upriver spawning areas. Consequently, rock blasting, clearance, and log-jam removal at these critical migration points was undertaken on at least eight occasions during the 1901–20 interval (Table 1).

We have mentioned above that as early as 1904 concern by both Native and non-Native peoples of Barkley Sound over the impact of the developing commercial sockeye fishery had led to a request for a hatchery. Consequently, the Henderson Lake hatchery was built at the head of Henderson Lake (Fig. 1) on Ternan Creek and was in operation by 1910. Initially, the hatchery concentrated on supplementing the natural production of Henderson Lake sockeye by incubating 8 to 10 million sockeye eggs annually and releasing the resultant fry into Henderson Lake. Because the record of Barkley Sound sockeye catches and escapement by stock in the early years of the hatchery's operation is incomplete (Fig. 3 and 4), it is difficult to gauge the precise impact of the hatchery on the Henderson Lake sockeye stock during this period.

SOCKEYE CATCH AND ESCAPEMENT 1901–20

1903 marks the beginning of the annual commercial pack statistics indicating the number of cases of sockeye put up in the Kildonan cannery. The pack of sockeye recorded at the Kildonan Cannery and attributed to Barkley Sound from 1903 to 1920 ranged from 385 to 7 309 cases (approximately 5 000 to 95 000 sockeye, Fig. 3a) and averaged 2 193 cases or 28 503 sockeye. There are no records during this period to identify the proportionate contributions of the three Barkley Sound sockeye stocks (Henderson, Great Central, Sproat) to the catch, but it was likely that the Henderson stock accounted for much of the catch given the following: the location of the cannery on Uchucklesit Inlet; the largely non-mechanized, terminal nature of the fishery, and the likelihood that the Somass stocks were still seriously depressed due to the frequent occurrence of both man-induced and natural blockages.

No quantitative records of escapement of any of the Barkley Sound sockeye stocks exist prior to 1917. Beginning in 1917, annual reports from the Henderson Lake hatchery include estimates of sockeye returning to the Henderson Lake spawning grounds (Fig. 4a) and, in accordance with anecdotal evidence offered above, suggest that both catch and escapement of sockeye may have been depressed in the years immediately prior to 1920 (Fig. 3a).

TABLE 1. A site specific chronology of conditions and fisheries interventions influencing sockeye salmon passage in the Somass watershed.

Stamp Falls	Events	Sproat Falls	Events	Papermill Falls	Events	Sproat Outlet	Events	GCL Outlet	Events
< 1912	NB	< 1901	NB	1893	MB	1866	MB	1930–31	MB, FR, FI
1912–13	NB, FI	1901	NB, FI	1895	MB	1957	MB, FR, FI	1957	MB, FR, FI
1915–16	NB, FR	1902	NB, FI	1898	MB, FR	1965	FR, FI	1965	FR, FI
1925	NB, FI, FR	1903	NB, FI	1902	MB, FI				
1926	NB, FI, FR	1914–15	NB, FI	1915–16	MB, FI				
1927	NB, FI	1934	NB, FR						
1931	NB, FI	1936	NB, MB, FI						
1932	FI	1950	NB, FI, FR						
1938	FI	1951	NB, FI						
1941	FI								
1942	FI								
1950	FR								
1954	FI								

NB = natural blockage
MB = man induced blockage
FR = fisheries study and recommendations
FI = fisheries intervention

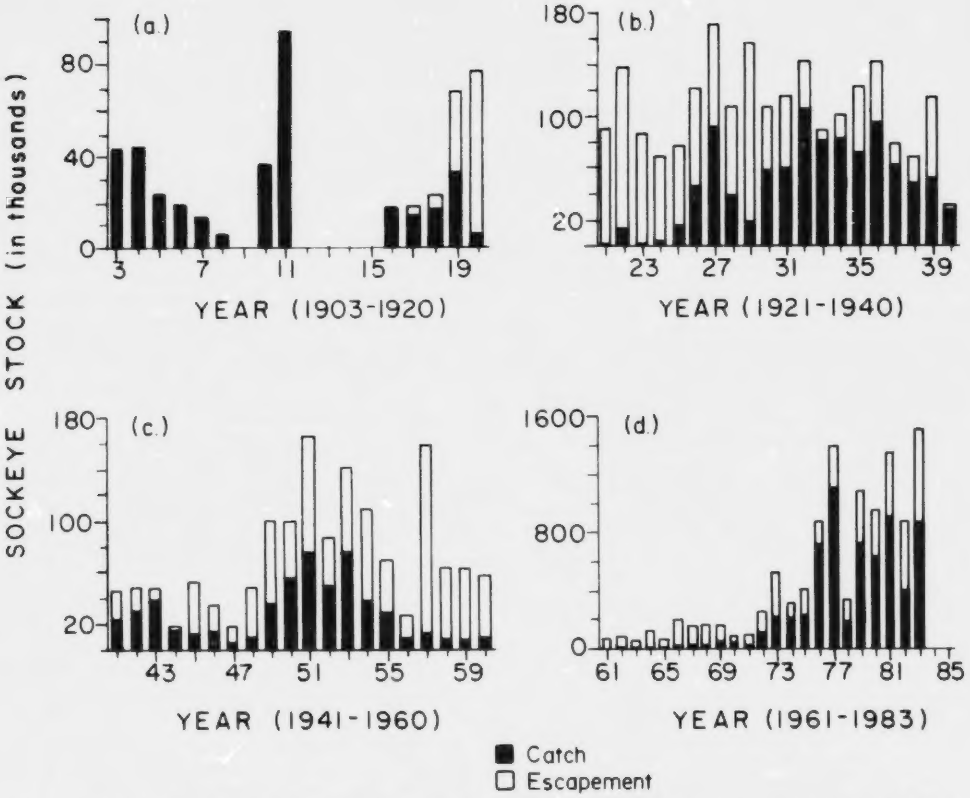

FIG. 3. Sockeye returns to Barkley Sound during the intervals (a) 1903–20, (b) 1921–40, (c) 1941–60, and (d) 1961–83. Qualifications are as follows: catches from 1903 to 1929 were recorded in each year as sockeye pack in cases. Case values were converted to estimates of sockeye numbers by assuming that 13 sockeye produce one standard case of 48 1-lb. tall cans. No catch record has been found for 1909 while records for 1912–15 inclusive have been omitted as they include large packs of non-Barkley Sound sockeye. Total numbers of Barkley Sound sockeye caught each year from 1930 to 1950 were tabulated by Clay (1950). Total numbers of Barkley Sound sockeye caught each year from 1951 to 1983 were tabulated from the annual record of B.C. Catch Statistics, DFO, Pacific Region. Values used here were total sockeye catches from Area 23 minus troll caught fish, which timing and size information suggest are principally Fraser River sockeye. Escapement estimates shown within each interval vary in degree of completeness. Escapements shown for 1917 to 1925 are for Henderson Lake sockeye only. From 1926 to approximately 1950, the escapement portion of stock is the sum of estimates from both Henderson and Great Central Lakes. From approximately 1951 to 1983, the escapement portion of stock is the sum of estimates from Henderson, Sproat, and Great Central lakes.

1921–40

OVERVIEW

This time period was characterized by continued expansion of resource based industries in the Alberni Valley and Barkley Sound region (Hill 1952). Substantial additions were made to both fishing fleet and processing plant capacity and were accompanied by increases in the average annual sockeye pack (49 370 fish, range 325 to 105 000) at Kildonan. Interventions by the Department of Fisheries occurred with much greater frequency to (i) protect salmon habitat, (ii) engage in sockeye stock enhancement via hatchery operations, (iii) solve fish passage problems, and (iv) exert more precise control over stock-specific catches through the regulation of subareas open to various components of the fishing fleet.

FISHERY DEVELOPMENT 1921–40

A number of forces operated during the 1920's to favour the expansion of sockeye fishing and processing capacity in Barkley Sound.

First, the practice of granting permits for exclusive fishing in certain districts between the years 1871 and 1921 was discontinued in 1922. This made it possible for those who had not previously operated on licensed grounds to fish. The limitation on the number of canneries which might be operated in B.C. was in force from 1908 to 1911 and from 1913 to 1917 but was also removed unconditionally in 1918. Thus, in 1923, on payment of the required fee, the business of salmon canning in British Columbia was thrown open to all qualified individuals or companies (Lyons 1969). These

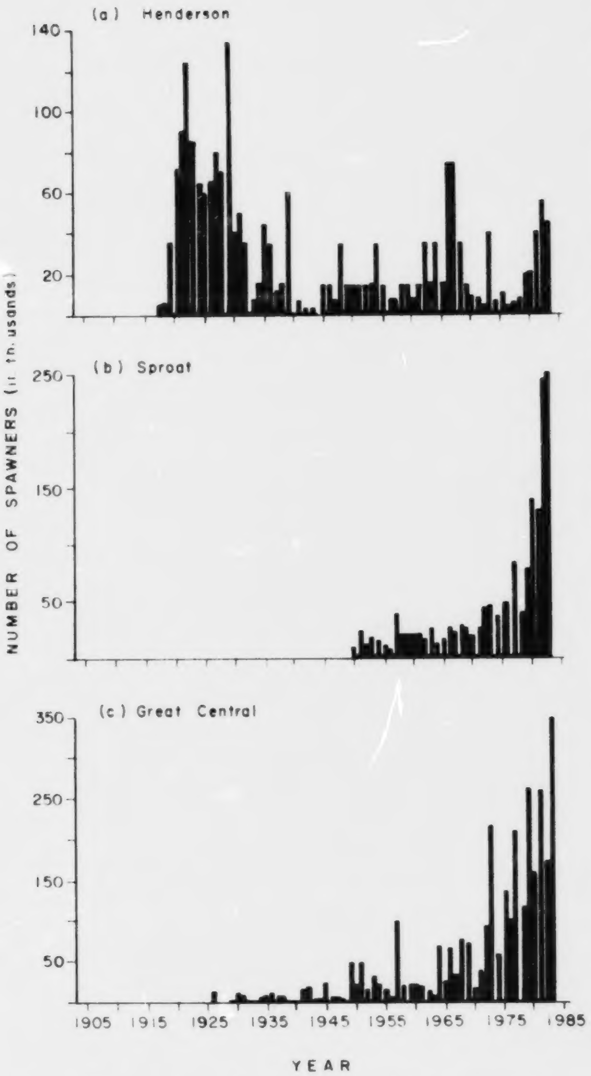

FIG. 4. Historical trends in annual sockeye escapements to (a) Henderson Lake, (b) Sproat Lake, and (c) Great Central Lake. Escapement estimates were assembled from a variety of both published and unpublished sources (see methods) and the values are reported here without adjustment. It is known that both procedures and effort levels associated with escapement assessments have changed systematically over the period of record. Consequently, values presented here should be viewed as indicative of only rather general trends in stock-specific escapements (Hyatt et al. unpublished observations). Few, if any, sockeye routinely reached Great Central Lake prior to construction of the Stamp Falls fishway in 1927. No quantitative record of sockeye returns to Sproat Lake prior to construction of the Sproat Falls fishway in 1950 has been found (b); however, evidence presented here indicates that sockeye returns to Sproat Lake were, with few exceptions, an annual event (see text for details).

forces were reflected in the Barkley Sound region by a number of events. The Millerd Packing Company established the Port Alberni Saltery in 1927 and a one-line cannery in 1929 to pack salmon (Lyons 1969). At Uchucklesit Inlet, the Kildonan Cannery and reduction plant were sold in 1928 by the British Columbia Fishing and Packing Company to B.C. Packers. Kildonan experienced rapid growth based upon both processing of salmon and especially the development of the pilchard fishery (*Sardinops caerules*).

Second, new markets for salmon products were developing and improvements to the region's transportation system aided movement of products to these markets. The Fisheries Overseer for the region stated with reference to 1927 that "a new feature is the shipping of fresh and cured salmon in (railway) car lots to the eastern states, some 20 cars going this way" (Wood 1927).

Third, increases in sockeye abundance relative to the 1901–20 period (Fig. 3a and b) appeared to promote increased fishing effort in the Barkley Sound region. Overseer Wood (1934) provided anecdotal evidence that returns of sockeye from 1926 to 1934 were unusually large as he states "Previous to 1926 our fishermen went to River's Inlet for the fishing season, now they stay at home from January to December and this year 120 of them took out gillnet licenses and 15 others came all the way from Westminster [sic] to engage in our sockeye fishing." Whether a cause or a consequence of the increased fishing effort, there is little doubt that the average catch of sockeye during the 1920–40 period had increased appreciably over that of 1903–20. (Compare Fig. 3a and b).

FISHERY REGULATION 1921–40

Early in this period, salmon regulations were made for only three geographical areas covering the entire B.C. coast. However, proliferating catching and processing capacity prompted creation of 27 new areas and establishment of area specific limitations on purse seiners. The number of purse seines operated on the B.C. coast in 1928 was 399; in 1929, the coastal limit was set at 371 spread among the management areas. Fisheries Overseers were also empowered to impose 24-h area closures in addition to the general 48-h closed period observed each week. These regulations effectively curtailed up to 20% of the fishing operations in a number of coastal areas in 1929.

Patterns of regulation in Barkley Sound followed the coastwide trend as restrictions on fishing locations were used with increased frequency to protect sockeye as they entered terminal areas. The closure of Uchucklesit Inlet and the Henderson River in 1920 was maintained through at least 1925. Similarly between 1921 and 1925, the fishing boundary at the head of Alberni Inlet was placed sufficiently far out to "prevent the fishing of Sproat and Stamp sockeye" in conjunction with initiatives by the Henderson Lake hatchery staff (see comments below) to build the sockeye runs up "to their original condition of productivity" (Ann. Rep. DMF 1926–27).

In addition to harvest by drag-seine, participation by both gillnetters and purse seiners in the Barkley Sound sockeye fishery had become firmly established with the result that regulations to control specific gear types appeared. In both 1928 and 1929, "the greater part of Alberni Canal" was closed to purse seiners to protect sockeye escapements (Wood 1928). Predictably, the result was a reduction in both the number and catch by purse seiners participating in the fishery. For example, in 1927 purse seiners had harvested 56 532 sockeye while gillnetters obtained only 8 911. However, with the exclusion of purse seiners from Alberni

Inlet in 1928, gillnetters caught 24 016 sockeye entering the Somass River and 15 196 sockeye at Henderson River. In addition, only 58 seine boats operated in the outside waters of Barkley Sound in 1928 by contrast with 88 in 1927. Purse seiners were regularly excluded from the inside waters of Alberni Inlet and Uchucklesit Inlet after 1929. Consequently, from 1929 to 1940, virtually all of the sockeye catch was taken by the gillnet fleet in terminal fishery locations.

HABITAT PROTECTION 1921–40

An increased rate of resource development in the Alberni Valley had the potential to create a number of problems for maintenance of commercially viable sockeye stocks. Fisheries personnel were faced with rapidly increasing logging with attendant potential for altering salmon habitats and by 1930 private interests had proposed tentative plans for construction of a high dam for power generation on the Stamp River. Bloedel, Stewart and Welch Ltd. began operating a sawmill which was supplied with logs from both sides of Great Central Lake and near many of its tributaries (Hill 1952). The mill site was located on Boot Lagoon at the Great Central Lake outlet. Great Central Sawmills Ltd. built a concrete pier and stop-log dam across the lake outlet in 1930 to allow logs to be towed from Great Central Lake to Boot Lagoon during the dry months of the summer. The channel between Boot Lagoon and the lake was also dredged to allow tugs to bring log booms to the Great Central mill site (Stockner and Costella 1980).

The dam elevated the surface of the lake about 2 m and raised concerns among fisheries personnel that salmon passage into the lake would be prevented or impeded and that the spawning grounds around the lakeshore would be ruined (Taylor 1929). Little could be done about the concern for alterations to the spawning grounds. However, at the insistence of fisheries personnel, the design of one of the outlet piers to the dam was modified to incorporate a fishway. During construction of the dam, it became apparent that this fishway would not function properly. Consequently, fisheries and construction personnel in the field devised a second fishway relying on the deployment of stop-logs and baffles. The Inspector of Fisheries, J. B. Wood, reported (Wood 1931) that the new fishway "worked well" to allow free passage of sockeye and coho to their spawning areas within Great Central Lake. Consequently, one of the runs of sockeye returning to the Somass River had been preserved through Departmental actions in the face of "industrial" development for at least the second time in its history.

SOCKEYE STOCK DEVELOPMENT 1921–40

Between 1921 and 1940, the Dominion Department of Marine and Fisheries engaged in concerted efforts to boost the productivity of Barkley Sound sockeye stocks both through stock enhancement initiatives associated with the Henderson Lake hatchery and through mitigation of sockeye passage problems within the Somass river system.

THE HENDERSON LAKE HATCHERY AND SOCKEYE ENHANCEMENT

During the initial phase of its operation (1910–21), the Henderson Lake hatchery was directed to increase production of Henderson Lake sockeye alone. However, as with many other hatcheries operated in B. C. at the time, it soon became a source of fry and eyed-eggs to be used in either supplementing weak runs of other sockeye stocks or in establishing new runs of sockeye to nursery lakes (Aro 1979). Consequently, from 1921 to 1941, the Henderson Lake sockeye stock and hatchery served as a source for outplants of approximately 50 million eyed sockeye eggs (Aro 1979; Withler 1982). The majority of these were planted in various tributaries of Sproat and Great Central lakes between 1921 and 1932 (Table 2) with the intention of supplementing production of natural stocks of sockeye in the former and of establishing a new stock of sockeye in the latter. The success claimed for these eyed-egg outplants in directly producing additional sockeye returns (Motherwell 1923; Ann. Rep. DMF 1932-33) is debatable given uncertainties over the status of the stocks of sockeye returning to Sproat and perhaps Great Central Lake prior to the hatchery egg-planting initiatives (see section below). However, it is certain that this enhancement enterprise helped raise an awareness of the potential for stock increases by sockeye returning to the Somass. This helped generate support for DMF initiatives to protect returning escapements in terminal areas as well as to solve sockeye passage problems (discussed below). These actions helped stabilize production gains exhibited by sockeye returning to Sproat and Great Central lakes during the latter period of the 1920's (Fig. 3b).

FISH PASSAGE PROBLEMS

Between 1901 and 1920, fisheries personnel had clearly identified the recurrent, difficult hydraulic conditions for sockeye passing Sproat and Stamp Falls on the way to the spawning grounds. Frequent rock blasting and log-jam clearance had provided some relief. However, the seriousness of the passage problems and their likely role in limiting sockeye production were revealed more clearly by a number of coincidental events beginning in the 1920's.

STAMP FALLS PASSAGE PROBLEMS

Beginning with the 1921 brood year, regular outplants of eyed-eggs from the Henderson Lake hatchery to tributaries of Great Central Lake (2.7 million eggs in 1921 alone) generated expectations that substantial numbers of adult sockeye might return to Great Central as early as 1925. In 1925, several thousand adult sockeye did appear at the base of Stamp Falls but their passage was blocked by low water from July to September and they died unspawned. The Inspector of Fisheries, E. G. Taylor, reported 5 000 sockeye in excellent condition in just one pool below the falls (Taylor 1925). Additional, unspawned, dead salmon were visible and

TABLE 2. Transfers of sockeye eggs and fry to the Somass River system (from Aro 1979).

					Distribution of eggs and fry												
					Eggs												Fry
					McCoy Lake	Great Central Lake							Sproat Lake				
Brood year	Collecting and eyeing hatchery	Source of eggs	No. of eggs collected by or transferred to distributing hatchery	Distributing hatchery	Heath Creek	Clark Point	Drinkwater Creek	Lindsay Bay Creek	Pine Point Creek	Polar Creek	View Lake Creek	White Pine Creek	Antler Creek	Gracie Creek	Snow Creek	Taylor River	Sproat Lake
1905	Fraser River	Upper Pitt River	100 000														
	Granite Creek	Scotch and Tappen creeks and Adams River	3 000 000	Fraser River													<250 000[a]
	Pemberton	Birkenhead River	4 500 000														
1906	Fraser River	Pitt River	24 000	Fraser River													75 000
	Pemberton	Birkenhead River	4 500 000														
1921	Henderson Lake	Clemens Creek and Henderson Lake beaches	10 033 000	Henderson Lake			1 344 000	112 000	448 000	336 000	448 000		80 000		112 000	1 120 000	
1922	Henderson Lake	Clemens and Ternan creeks and Henderson Lake beaches	8 505 000	Henderson Lake	250 000	182 000	912 000	119 000			343 000	440 000			112 000	1 344 000	
1923	Henderson Lake	Henderson Lake beaches	8 505 000	Henderson Lake	252 000		1 008 000			434 000	140 000	420 000		574 000		1 428 000	
1924	Henderson Lake	Henderson Lake beaches	8 543 000	Henderson Lake	252 000		1 008 000			336 000		658 000		455 000		1 547 000	
1925	Henderson Lake	Clemens Creek and Henderson Lake beaches	8 505 000	Henderson Lake	252 000		1 008 000			441 000		553 000				2 002 000	
1926	Henderson Lake	Clemens Creek and Henderson Lake beaches	8 505 000	Henderson Lake			1 386 000			336 000		280 000				2 002 000	
1927	Henderson Lake	Henderson Lake beaches	8 550 170	Henderson Lake			2 002 000									2 002 000	
1928	Henderson Lake	HendersonLake beaches	8 799 000	Henderson Lake			1 442 000			560 000						2 002 000	
1929	Henderson Lake	Henderson Lake beaches	8 505 000	Henderson Lake			1 505 000									2 002 000	
1932	Henderson Lake	Henderson Lake beaches	7 532 000	Henderson Lake			2 002 000									1 505 000	

[a] 250 000 fry were released in Henderson, Kennedy, and Sproat lakes.

many salmon at the base of the falls appeared to be considerably battered from their efforts to surmount the falls. Taylor recommended "brailing" salmon by hand over the falls in subsequent years as "under the present conditions it is unlikely that one sockeye salmon gets over the falls." Late in 1925, work was performed to remove protruding rock from the crest of the main falls at Stamp River. Pockets were excavated on the right bank to "assist the ascent of fall salmon" into Great Central Lake. The report by J. Mchugh, the resident engineer, on the rockwork completed in 1925 was that "the efforts were successful as far as the passage of coho and steelhead are concerned but it cannot be hoped that sockeye salmon can ever reach Great Central Lake until the larger and more comprehensive scheme (for a fishway) is executed" (Ann. Rep. DMF 1925).

In 1926, thousands of adult sockeye again appeared at the base of Stamp Falls only to be blocked by low water conditions. Following recommendations made in 1925, a crew of men employing dip nets passed 11 000 sockeye safely over the falls. Unfortunately, thousands more sockeye died below the falls, unspawned (Ann. Rep. DMF 1926–27).

The apparent success in establishing a stock of sockeye to return to Great Central Lake, along with their blockage and high mortality at Stamp Falls in 1925 and 1926, provided a strong rationale for funding requests to Ottawa to permit construction of a professionally engineered fishway at Stamp Falls in 1927. The cost was $ 7,015.58, 648 cubic yards of rock were excavated, and 91 cubic yards of concrete were poured. Salmon arriving after the completion of the work passed up through the fishway without difficulty. (Ann. Rep. DMF 1927–28).

The fishway was completed in September. However, the main body of the sockeye run negotiated Stamp Falls between June and August in the absence of the fishway, despite previous claims that Stamp Falls was entirely impassable to sockeye. Thus, the events in 1927 raised three interrelated questions that have never been fully resolved. These are: (1) Were the eyed-egg outplants from the Henderson Lake hatchery responsible for establishing a new sockeye stock in Great Central Lake? (2) Was Stamp Falls totally impassable to adult sockeye prior to 1927? and if not (3) Was construction of the Stamp Falls fishway essential for the development and maintenance of a commerically viable sockeye stock returning to Great Central Lake?

A combination of historical observations and new quantitative analysis of the nature of sockeye passage problems in the Somass system (Hyatt and Radziul, unpublished data) have shed considerable light on these questions. First, extensive records of direct obervations of fish passage over at least a 20-yr interval after completion of the Stamp Falls fishway indicates that adult sockeye were able to ascend in many years (1929–31, 1938–39, and 1943–45), under a restricted range of hydraulic conditions, without relying on the fishway. Thus, it is likely that Stamp Falls never represented an absolute barrier to sockeye. Records of sockeye passage at Stamp Falls show the range of discharge within which adult sockeye could ascend in the absence of a fishway and, in combination with time series data on daily discharge from the Stamp River between 1914–72 (Water Survey of Canada), lead us to conclude that Stamp Falls would have been virtually impassable in as many as 22–36 of the 56 years of record. Further, during the main period of sockeye migration in the Somass River (June 1 to Aug. 31 inclusive), it appears that in years when passage was possible, fish could have ascended Stamp Falls on average 28 of 92 days.

Without the Stamp Falls Fishway, it is likely that production of sockeye in Great Central Lake would have been an intermittent affair frequently punctuated by loss of entire brood lines or, over long intervals, stock extinctions. Perhaps the best circumstantial support of this assessment is the absence of Indian reserves, archaeological sites, and ethnographic references to the Stamp River above Stamp Falls. This suggests that prehistorically the upper reaches of the Stamp River were not easily accessible to large runs of salmon. Such runs would clearly have been an attraction for Native peoples to establish fishing sites such as those readily discernible on the Sproat and lower Somass rivers (McMillan and St. Claire 1982). Thus, there is little doubt that the Stamp Falls fishway has been a critical factor in providing adult sockeye with access to Great Central Lake annually since 1927. Clearly the effort and expense of both the construction and periodic maintenance of this fishway (Table 1) have been sound investments. By contrast, it is not possible to determine whether or not the eyed-egg outplants originating from the Henderson Lake hatchery were solely responsible for establishing the Great Central Lake sockeye stock (Harrison 1922).

SPROAT FALLS PASSAGE PROBLEMS 1921–40

The difficult passage of adult sockeye to the Sproat Lake spawning grounds had been identified as a potential impediment to stable production as early as 1901 (Ann. Rep. DMF 1902). However, passage problems at Stamp Falls overshadowed those at Sproat Falls. Observations of sockeye passage difficulties or a requirement for clearance work at Sproat Falls in each of 1931, 1934, and 1936 raised enough concern that in 1936 detailed observations were made "for the purpose of gathering reliable data to permit an intelligent report and recommendation being furnished at the end of the season" (Tait 1936). The observations revealed that large numbers of sockeye originating from Sproat Falls were returning down the Somass River unspawned and badly bruised. Tait's report noted that dead and unspawned sockeye were found each year in the river below Sproat Falls but that in 1936 far more were noticed, evidently because the run was larger than in any previous year, and water was fairly high. The removal of log jams at the crest of the falls appeared to alleviate most of the passage problem and no further actions were taken.

CATCH AND ESCAPEMENT 1921–40

Barkley Sound catch and escapement patterns from 1921 to 1940 (Fig. 3b) were the product of several opposing trends. Removal of restricted entry into coastal salmon fisheries, and the accompanying fleet expansion had the potential to increase fishing effort and, at least in the short run, increase sockeye catch rates. By contrast, fishing restrictions to protect sockeye on the final approaches to their rivers of origin had the potential to reduce catch rates in the short run and thereby to increase total stock production in the long run. Finally, initiatives such as the Henderson Lake sockeye hatchery and improved sockeye passage at Stamp Falls had the potential to influence both the short and long term productivity of the Barkley Sound sockeye stocks. A number of inferences are possible concerning the relative influence of these events on the stocks.

In spite of the trend toward fleet expansion from 1920 to 1929, the average catch in Barkley Sound was no greater than it had been between 1903—20 (Fig. 3a and b). This was undoubtedly due to the complete closure of Uchucklesit Inlet, the Henderson River, the head end of Alberni Inlet (1920-25), and, to purse seines only, the greater part of Alberni Inlet (1928-29). These actions plus the sockeye hatchery at Henderson Lake and the fish passage facility at Stamp Falls were intended to increase escapements and there is little doubt that they were successful. Henderson Lake escapements increased immediately and remained high after closure of the Uchucklesit Inlet fishery (Fig. 4a). Although few if any sockeye had escaped to Great Central Lake prior to 1926, they were counted in increasing numbers at the Stamp Falls fishway after 1927 (Fig. 4c) and observations by fisheries personnel suggest a similar pattern of increased escapements to Sproat Lake during this interval. Further, beginning in 1919, total returns of sockeye to Barkley Sound increased substantially (relative to the lows of 1916-18) and were sustained for at least the next 20 years (Fig. 3a and b). The Henderson Lake hatchery may have initiated this increase since it occurred years before either increased escapements or 1927 improvements at Stamp Falls could have contributed to adult returns (1923-31) in Barkley Sound.

Although the reasons were perhaps not as well understood as they are now, it was apparent to departmental field personnel by the late 1920's that the Barkley Sound sockeye stocks had increased and that the increase appeared to be sustainable in the face of increased fishing pressure. Fisheries Overseer J.B. Wood described the fishing seasons of 1927 and 1928 as "banner years" for Barkley Sound salmon and stated in reference to sockeye returns that "from every angle the season [of 1927] was the most successful in fifteen years" (Wood 1927, 1928). Indeed, in 1929 when the catch dropped to approximately 20 000 sockeye but the total escapement rose to almost 140 000 sockeye, Wood complained that a greater catch could have been achieved if more gillnetters had participated and used better fishing gear (Ann. Rep. Can. Dept. Fish. 1929-30). This deficiency appears to have been short-lived as between 1930 and 1940 the average annual catch of Barkley Sound sockeye was approximately 74 000 fish. In 1932, for the first time, the fishery achieved a single-season catch in excess of 100 000 fish. Since the 1920-30 aggregate-stock increase did not continue during 1930-40 (Fig. 3b), the apparent exploitation rate on the Barkley Sound sockeye must have increased from an average of approximately 20% during 1921-30 to over 60% during 1930-40.

A precise breakdown of the composition of the catch according to stock of origin is not available from 1921 to 1940. However, a number of observations suggest that the Henderson Lake stock was dominant in the first half of the period with the Sproat and Great Central stock contributions increasing in importance during the latter half. First, chronic problems for fish passage at Stamp Falls (prior to 1927), Papermill Dam (prior to 1915-16), and Sproat Falls (prior to 1950) precluded any significant contribution of Great Central Lake sockeye, and likely limited the contributions of Sproat Lake sockeye to Barkley Sound sockeye production and catch. In support of this, temporary closure of the Uchucklesit Inlet–Henderson River sockeye fishery between 1921 and 1925 resulted in escapement increases at Henderson Lake that were roughly as large as the entire Barkley Sound catch prior to closure. This suggests that much of the catch before 1926 was of Henderson Lake origin. In addition, from 1926 to 1934 J.B. Wood kept separate records of the catch in the terminal fishing areas of Uchucklesit and Alberni inlets as part of the effort to record productivity of the Somass stocks. These records indicate (Table 3) that the relative contribution of the Henderson stock to the Barkley Sound total may have decreased during this interval but that it still contributed on average approximately 32% of the catch.

TABLE 3. A comparison of stock composition in the Barkley Sound sockeye catch during (a) 1926-34 (data from Wood 1934) and (b) 1979-84 (Hyatt, unpublished data).

Year	% Henderson	% Somass	% Great Central	% Sproat	Total Catch
(a) 1926	77.3	21.8			45 812
1927	28.2	71.8			91 069
1928	39.5	60.5			38 000
1930	18.1	81.9			58 600
1931	34.2	65.8			59 260
1932	26.7	73.3			105 000
1933	25.5	74.5			80 500
1934	8.0	92.0			81 500
Mean	32.2	67.7			69 968
(b) 1980	4.4	95.6	52.7	42.8	642 800
1981	2.9	97.1	59.1	38.1	1 009 429
1982	2.1	97.9			476 185
1983	4.6	95.4	55.3	40.1	919 377
1984	5.2	94.9	59.7	35.2	818 497
Mean	3.8	96.2	56.7	39.1	773 258

1941-60

OVERVIEW

During this period events would illustrate the extent to which development and control of the Barkley Sound sockeye fishery had become linked to social and economic forces operating at levels ranging from local to international. High demand for canned salmon during the war years (1940-45) combined with unlimited licensing and unregulated entry of gear into the coastwide salmon fisheries resulted in substantial increases in both the size and efficiency of the salmon fleet. Regardless, the catch of salmon on the coast did not increase. In Barkley Sound, catches and the total stock of sockeye declined in association with (i) closure of the Henderson Lake hatchery and (ii) the elevated exploitation rates of the late 1930's. Thus, during this period, Federal fisheries personnel faced the classic dilemma of maintaining runs within the context of high demand and reduced stock size. They responded by further refining in-season controls on the spatial and temporal deployment of the fishing fleet while continuing regular interventions to protect salmon habitat and to advance stock development activities. Fisheries research and management made significant contributions to both of the latter activities.

FISHERY DEVELOPMENT 1941–60

Political and economic forces made this one of the most volatile periods in the development of both the coastwide salmon industry and the Barkley Sound sockeye fishery. Information compiled from Lyons (1969) indicates that development of the coastwide salmon fishery took place within the context of extreme fluctuations in (i) demand for product, (ii) availability of the raw resource, and (iii) competition for the raw resource.

During the war years (1940–45) canned salmon was in great demand, spurring efforts to maximize production. New gear continued to enter the salmon fisheries and many processing plants were expanded and improved. No labour strikes disrupted the industry's ability to generate product. By contrast with the stability of the war years, 1945–60 was characterized by labour unrest and large fluctuations in both the supply and demand for salmon. Strikes idled the fishing industry and influenced its success in effectively harvesting fish for portions of 1945, 1949, 1952, 1954, 1957, and 1959. The high demand of the war years was followed alternately by low and then high demand for salmon as export markets first shrank and then expanded rapidly along with postwar economies.

Throughout 1941–60, competition within the expanding fishing fleet proved a potent force for promoting technological innovation to improve the fishing power of individual vessels. The use of hydraulic power blocks (for handling seines), hydraulic drum seines, and synthetic fibre nets all became commonplace. Keen competition among processors to supply volatile export markets cut profit margins and continued the strong trend, initiated between 1927 and 1940, toward consolidation of plants. This trend was aided by rapid transport of fish on power driven packers with holding tanks containing refrigerated seawater. Consequently, between 1941 and 1960 the number of operating salmon canneries fell from 36 to 23 (Fig. 2).

Many events characterizing development of the Barkley Sound sockeye fishery during the 1941–60 period mirrored these coastwide patterns. Exploitation rates, total catch, and escapements all exhibited much greater fluctuations (see details below) than during 1921–40. After the war, British Columbia Packers Ltd. initiated collection of salmon with packer vessels from outlying regions on the coast and sent them to its Imperial Cannery at Steveston (Paterson 1979). The plant and wharves of the Kildonan Cannery on Uchucklesit Inlet were badly damaged by an earthquake in 1946. This event, along with the drive to control production costs, led B. C. Packers to close the Kildonan Cannery and rely on packers to transport Barkley Sound sockeye to their Steveston plant for processing. The gillnet fleet adopted nylon gillnets for Barkley Sound fishing in 1954 although comments in the Annual Narrative Report suggest that nets were not especially successful in fishing for sockeye that year.

FISHERY REGULATION 1941–60

Unregulated entry of increasingly efficient gear into the fishery and asynchronous changes in market demand and salmon supply called for progressively more precise in-season management of the returns of salmon. Consequently, in 1950 the Department of Fisheries initiated a coastwide system of 30 statistical areas to both control and retrieve records of catch and escapement, and a sales slip system was implemented to provide a corresponding breakdown of catch by gear, species, number, and weight. This system, with minor modifications, has remained in place up to the present time (McDonald 1981). Further, in order to discourage catches by net fisheries of stocks of unknown origin in offshore waters, a "surf line" regulation was implemented in 1958 such that all net fishing for salmon was to be conducted inside of boundaries drawn from headland to headland in each statistical area.

Barkley Sound and Alberni Inlet were designated as statistical area 23 and divided into 10 subareas (Fig. 1). The surf line extended from Amphitrite Point in the north to Cape Beale in the south. Subarea openings and closures were used during the fishing season with increasing frequency to manage the mixed stock fishery for sockeye in Barkley Sound, Uchucklesit Inlet, and Alberni Inlet. For example, although crude subarea openings and closures had been used to manage the Barkley Sound stocks during the 1920's and 1930's, a single pre-season announcement of fishing boundary regulations usually lasted for the entire season. By contrast between 1951–60 additional within-season announcements of changes in subarea openings and closures occurred in 6 out of 10 years (Hyatt and Raymond, unpublished data). Openings and closures favoured exploitation or conservation of each of the three Barkley Sound sockeye stocks as required. Improved knowledge of stock return-timing also permitted greater precision in directing the gillnet fishery to individual stocks.

The Barkley Sound managers also used subarea openings and closures to solve problems affecting the fishing fleet. For example, annual narrative reports and area history summaries first comment on basking shark (*Cetorhinus maximus*) damage to troll gear and nets in 1955, and are followed by entries in 1956, 1957, and 1958 when "basking sharks were present in large numbers" and "considerable net damage occurred during the sockeye fishery". In 1959 and 1960, the Alberni Inlet fishing area was extended to China Creek "to allow an area where sharks are less numerous" and to reduce damage to fishing gear.

HABITAT PROTECTION 1941–60

Habitat issues in previous time periods had been relatively straightforward involving acute or obvious potential impacts on salmon rather than chronic and subtle ones. This was not entirely the case for the 1941–47 period. In particular, a proposal by Bloedel, Stewart and Welch Ltd. to build a Kraft pulpmill in Port Alberni raised concerns over the impact that discharge of pulpmill effluent into Alberni Inlet might have on both juvenile and adult salmon utilizing the inlet as a rearing area and migration path. Although the proposal was first raised in the late 1930's, the development was not executed until 1947. During the interim, scientists from the Fisheries Research Board conducted pioneering oceanographic research on Alberni Inlet (Tully 1949) and, partly as a result of these studies, the mill was built at the head of Alberni Inlet. The mill outfall was designed to discharge the effluent at the sea surface so that it would mix

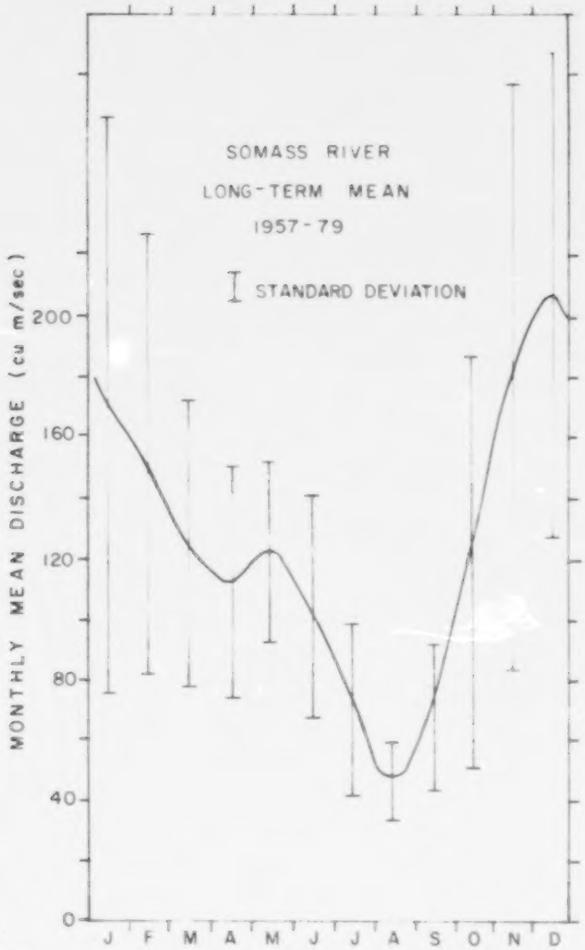

FIG. 5. Monthly mean discharge for the Somass River between 1957 and 1979. Data extracted from records of Water Survey of Canada.

with the water in the surface layers. The density of the effluent was approximately equal to that of fresh water so that once discharged through the outfall, the effluent remained above the dense saline layer (Morris and Leaney 1980).

Tully developed a relationship between Somass River discharge and dissolved oxygen concentration which he suggested could be used in the control of pollution and so minimize any impact on salmon in Alberni Inlet, especially during the naturally low flow period of late summer (Fig. 5). Consequently, in the mid 1950's, when Fisheries Department personnel responded to a request for expansion of the pulpmill at Port Alberni, one of their recommendations was that MacMillan Bloedel Ltd. replace the storage dam built in 1930 at the outlet of Great Central Lake as a condition of approval for increased effluent discharge related to pulpmill expansion (Clay 1955; Whitmore 1957). The storage dam at Great Central Lake and a weir immediately below the Sproat Lake outlet were built in 1957. These structures provided enough flow control over the Somass River at Port Alberni to dilute pulpmill wastes to safe levels for salmon. Regulations required a minimum flow of 940 cfs at the mouth of the Somass River. In addition a 19 baffle, vertical-slot, fishway and barrier dam about 30 m downstream of the old dam were incorporated into the new design to assure easy passage of sockeye into their Great Central Lake spawning grounds. The Barkley Sound sockeye stocks had entered an era during which tightly focused research would increasingly be used to solve habitat protection, stock management, and stock development problems.

SOCKEYE STOCK DEVELOPMENT 1941-60

Closure of the Henderson Lake hatchery in 1935 appeared to alter the prospects for sockeye stock development in the early 1940's. Consequently, these activities focused entirely on increasing escapements and further assessment and mitigation of sockeye passage problems within the Somass River system.

APPARENT IMPACT OF CLOSURE OF THE HENDERSON LAKE HATCHERY

After the fishing season of 1933, the Department of Fisheries announced its intention to stop operating salmon hatcheries in British Columbia. This decision was based upon scientific data, accumulated over a period of years, showing that hatchery propagation of salmon for the benefit of the commercial fishery did not warrant the cost involved (Aro 1979). Therefore, after the season of 1934, three salmon hatcheries were closed, followed by eight more at the end of 1935. All salmon hatcheries in British Columbia were formally closed on December 31, 1937 (Lyons 1969).

No rigorous assessment of the impact of either the operation or closure of the Henderson Lake hatchery on its sockeye was ever undertaken. However, we do know that the combination of hatchery operations and fishery regulations to protect Henderson fish in terminal fishing areas permitted the Henderson stock alone to account for total returns of sockeye of between 40 000 and 140 000 fish from 1919 to 1926 (i.e., years prior to the development of large stable returns to the Great Central and Sproat Lake stocks). Sustained stock returns as large as these have apparently not been observed for the Henderson stock since the closure of the hatchery in 1935. Given the four to five year life span of Henderson sockeye, any impact of hatchery closure on stock size would have begun to materialize in the return years beginning with 1938 and indeed the record does show an apparent decline in both catches and escapements of Barkley Sound sockeye beginning in the late 1930's and lasting into the late 1940's (Fig. 3c). Some of this decline may have been more apparent than real due to a substantial reduction in the effort expended to enumerate the escapement portion of the Henderson stock (Fig. 4a) through the years after hatchery closure (Hyatt, unpublished data). However, the decline and continued low catches during the high demand war years remains as a tantalizing piece of evidence that closure of the hatchery did have a negative impact on production of Barkley Sound sockeye.

FISH PASSAGE PROBLEMS

Stamp Falls

Construction of the Stamp Falls fishway in 1927 and stabilization of sockeye access to Great Central Lake in the years immediately thereafter (Wood 1929; Fig. 4c) were followed by concerns over the deterioration of the fishway in the early 40's. In 1941, a division wall of the fishway was completely broken through and major repairs were made including the addition of new timber gates to control fishway water levels (Ann. Rep. Dept. Fish. 1941–42). The fishway was again damaged during the winter of 1942 and required additional repairs to one of the concrete compartment walls. In 1950, abnormally high water levels blocked passage of sockeye at the base of both Stamp Falls and the fishway, suggesting the need for further modification. Given evidence for deterioration of both the structure and performance of the fishway, a new 37 baffle (149 m long), vertical-slot, fishway was installed at Stamp Falls in 1954 thus ensuring continued easy access of sockeye to Great Central Lake.

Sproat Falls

Although observations of delayed migration of sockeye at Sproat Falls had been made as early as 1901, problems there had generally been overshadowed by those at Stamp Falls. In the early 1940's, this once again appeared to be the case. However, the abnormally high water levels of 1950 produced concentrations of adult sockeye not only at Stamp Falls but also at the base of Sproat Falls. The blockage of sockeye passage at the latter site appeared serious enough that fisheries personnel used hand-nets to pass sockeye over Sproat Falls. A research project was also initiated in 1950 to assess the seriousness of the Sproat Falls passage problem by recording the migration progress of sockeye tagged in the Sproat River below the falls (Clay 1950). The tagging indicated that sockeye were delayed at the falls for periods of up to 31 days and that 50% or more of the run could have been delayed by 10 days or more. During the delay, the fish were subjected to injuriously high temperatures. Some fish died attempting to surmount the falls. The carcasses of many unspawned fish were found during surveys at Sproat Lake. Since these fish lacked any outward signs of damage it was assumed that the mortality was mainly due to delay and high water temperatures at the falls (Clay 1950). It was recommended that a fishway (which would be operable at flows from 50 to 2 000 cfs) be constructed on the left bank of the river at Sproat Falls, and in 1951, a 15 baffle, vertical-slot, fishway was completed at a cost of $50,000.

The Sproat Falls fishway made a twofold contribution to sockeye stock development. First, it relieved sockeye passage problems which, although less serious than those at Stamp Falls prior to 1927, did reduce the potential productivity of Sproat sockeye in a number of years. Our recent analysis of the relationship between discharge and sockeye passage problems at Sproat Falls (Hyatt and Radziul, unpublished data) indicates that without the fishway, passage problems as severe as in 1950 would have occurred in only 5 of the 56 years of record. Fish passage would have been entirely free of blockage in 27 of the 56 years. Further, during the main period of sockeye migration (June 1 to Aug. 31, inclusive), it appears that fish passage at Sproat Falls would have been possible each year on average for 84 days out of 92. Thus, construction of the Sproat Falls fishway did not rival the contribution to sockeye stock development made much earlier with the building of the Stamp Falls fishway. However, a second contribution which should not be overlooked is that it provided, for the first time, a viable location for quantitative estimates of the Sproat Lake sockeye escapements (Fig. 4b) and heralded a period of stock development through more precise management of escapements of Barkley Sound sockeye.

CATCH AND ESCAPEMENT TRENDS 1941–60

The general pattern for both catch and escapement from 1941 to 1960, relative to the preceding period (1921–40), was of a substantial decline followed by a moderate resurgence and then another decline (Fig. 3c). A number of these trends in catch and escapement are readily identifiable as having been influenced by specific events associated with changes in fishery development, fishery regulation, or stock development patterns. We have suggested above that the low catch and escapements observed in the early 1940's were a likely consequence of reduced productivity of the Henderson Lake sockeye stock as a result of the closure of the Henderson Lake hatchery. By contrast, the exploitation rate between 1940 and 1944 was higher on average at 71.3% than in any previous period of record. The high demand for canned salmon during the war years was likely responsible in part as exploitation rates on Barkley Sound sockeye dropped during the postwar years.

Larger escapements, especially in the immediate postwar years relative to the war years, appear to have promoted a stock resurgence beginning in 1948 and lasting through the early 1950's. As the stock size rose and then fell between 1948 and 1960 so too did the maximum number of gillnetters involved in the fishery (Fig. 6). Thus, the prolonged interval of unlimited gear entry into coastal salmon fisheries in general and the Barkley Sound sockeye fishery in particular, appears to have created fleet capacity which would respond to even modest changes in stock size at locations such as Barkley Sound as early as the 1940's. Variations in sockeye abundance, expressed either as catch or total stock, in Barkley Sound were generally followed by rapid adjustments in fleet size (Fig. 7a and b).

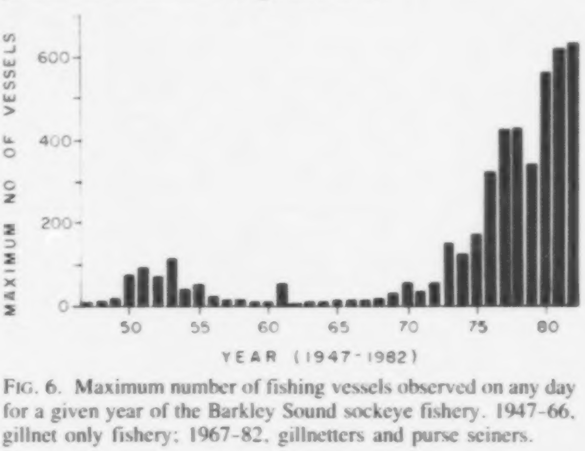

FIG. 6. Maximum number of fishing vessels observed on any day for a given year of the Barkley Sound sockeye fishery. 1947–66, gillnet only fishery; 1967–82, gillnetters and purse seiners.

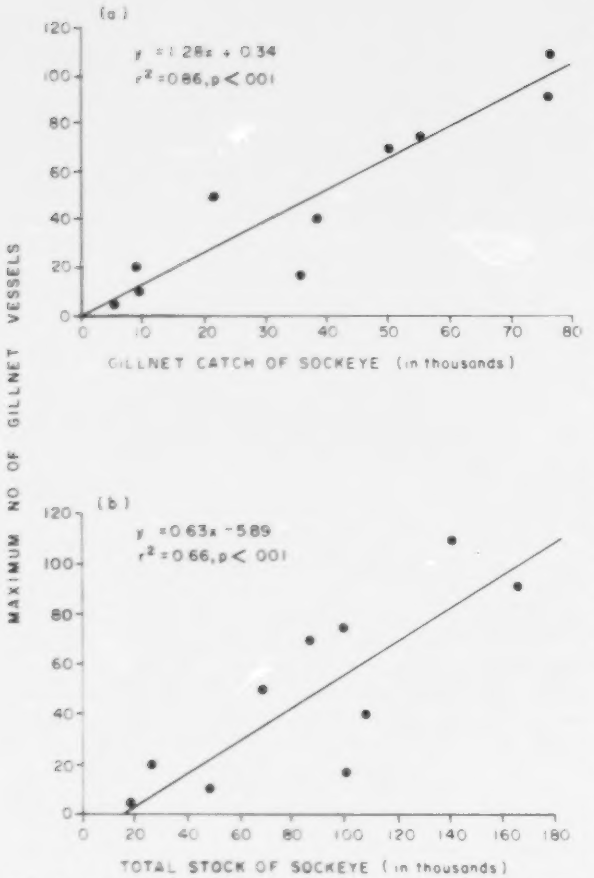

FIG. 7. Relationships between annual variations in the maximum number of gillnetters participating in the fishery and annual variations in sockeye abundance as indexed by (a) catch or (b) total returns between 1947–56.

The period 1957–60 was excluded from the analysis above due to a number of exceptional factors that tended to disrupt the normal association between fleet size and sockeye abundance. First, fishing strikes in 1957 and 1959 idled much of the fleet with the result that seasonal exploitation rates were artificially low in those years (< 15%). During 1957, the strike extended from June 22 to July 3rd, and a record escapement of sockeye reached Great Central Lake (Fig. 4c). Second, 1957–60 was a period of unusual ocean climate (Fulton and LeBrasseur 1985) and this affected the fishery. Basking sharks were present in such abundance and did so much damage to gillnets that fishery managers moved the fishing boundary further up Alberni Inlet to reduce gear loss. In addition, during 1958 the sockeye were unusually late in returning to Barkley Sound and a major portion of the escapement did not reach the Somass River until September, i.e., 2 months later than average. Thus, it is not surprising that both the catch and the number of fishing vessels were low (averages of 8 986 fish and 12 gillnetters, respectively) in spite of stock sizes that were well above average during these years.

For the years 1941–60, it is especially difficult to unequivocally partition the relative contributions of the Henderson, Sproat, and Great Central Lake sockeye stocks to the Barkley Sound sockeye catch. Other than the records of escapements returning to each stock (Fig. 4a, b, and c), there is no quantitative record of their relative performance. Further, the escapement estimates do not permit discrimination of any differences in stock size less than approximately two fold, as the assessment procedures used to obtain the escapement estimates are known to vary in accuracy from stock to stock (Hyatt et al., unpublished data). Regardless, the qualitative assessment of fisheries guardians, patrolmen, and managers during the interval was that the Henderson stock contributed the major portion of sockeye catch in most of the years between 1941 and 1960.

Entries in both Annual Narrative Reports and Area History Summaries indicate that field personnel believed that the Henderson Lake stock accounted for most of the catch in the years 1951–56. In the latter year, the observation was made that "for the first year in some time there has been a noticeable decline in the Henderson run" (Annual Narrative Report 1956). However, the same report still places the relative contributions of Henderson and Somass sockeye to the total catch for this year of apparently low Henderson returns at 60% and 40%, respectively. These same records suggest a reduction in the relative catch of the Henderson stock from 1957 through 1960 and a marked increase in the contributions of the Somass stocks.

Although the basis for attributing catch to stock of origin is not well documented, the annual records do indicate that these assessments relied upon (i) the largely terminal nature of the gillnet fishery in small subareas (e.g., Somass River mouth, Uchucklesit Inlet) of Barkley Sound and (ii) detailed daily observations of stock return timing by river guardians stationed at numerous locations such as Kildonan, Port Alberni, and Stamp Falls. For example, there is ample evidence in our recent analysis of diaries and end of week reports of fisheries officers and river guardians that they followed the return timing of the Henderson stock to Uchucklesit Inlet closely (on virtually a daily basis during late summer to early winter when guardians were resident at Kildonan) and that it was well understood that sockeye of this stock returned approximately 4–6 wk later than those of the Somass (Hyatt, unpublished data). The spatial distribution of the small fishing fleet and specific groups of sockeye entering Alberni Inlet were also followed closely. For example, when Henderson Lake sockeye were returning, the gillnet fleet often concentrated its efforts within the bounds of Uchucklesit Inlet or moved in and out of the inlet in concert with the fish, as they responded to changing weather conditions. Consequently, it may be tentatively concluded that the Henderson sockeye stock was the mainstay of the Barkley Sound sockeye fishery through most of the years between 1941 and 1960.

1961–83

OVERVIEW

This was an interval of relative stability in the coastwide salmon fishing and processing industry. Fisheries research and management joined forces to achieve spectacular advances in development and regulation of Barkley Sound sockeye stocks. This interval is also the best documented of any to date. Major activities included research on the potential impact of deteriorating water quality in Alberni Inlet on salmon production, successful lake fertilization which increased sockeye production to unprecedented levels, a rapid response by the fishing fleet to a new source of fish, including transition to a mixed gear fishery, refinement of regulations covering openings by time period and subarea, refinement of techniques for partitioning stocks (e.g., parasite identification), and management to achieve optimal escapement and stock production under a continuing regime of lake fertilization.

FISHERY DEVELOPMENT 1961–83

The coastwide salmon fishery exhibited many signs that the industry had achieved a new level of maturity. This was a period of relative stability of supply and demand and responsiveness by the fishing industry to meet both of these conditions. Packs of salmon were average to above average and were accompanied by a generally uniform demand with strong export markets for canned sockeye. Towards the latter part of the period, the fresh and whole frozen-fish markets exhibited increased demands at both the national and international level. Labour relations in the industry were markedly less chaotic than in the interval from 1941 to 1960. There were fewer strikes and they were of shorter duration, notably in 1963, 1971, 1973, and 1975. However, no strikes disrupted the fishing seasons between 1964 and 1970 during which there was the unprecedented occurrence of two, 2-yr agreements (1965–66, 1967–68) concerning wages and prices to be offered for raw fish. The rapid consolidation that characterized the fish processing sector between 1925 and 1950 was not evident during the 1961–83 interval and the number of operating canneries was relatively constant (Fig. 2).

The Federal Government, recognizing the unique nature of the West Coast Salmon Fishery, commissioned a report to examine the related issues of limited entry and the economics of the salmon fishery (Sinclair 1960). The "Sinclair Report" was presented to Parliament in the early 1960's. However, its recommendations proved unacceptable to the fishing industry of B.C. and politically unpalatable (Lyons 1969). Overcapacity of the fishing fleet relative to the supply of fish had become a chronic (Pearse 1982) and apparently insoluble problem.

Events associated with the development of the sockeye fishery in Barkley Sound during this time period stand in stark contrast to those exhibited by other salmon fisheries on the coast. The period stands out as remarkable from start to finish. Initially the DFO focus was on habitat protection and stock conservation. However, before the period ended, the Barkley Sound sockeye fishery had been transformed from one of many small to medium sized sockeye fisheries (average annual catch 1941–72 of 30 129 fish) on the outer coast, to the third largest producer of sockeye in the province (average annual catch 1973–83 of 568 310 fish), surpassed routinely by only the sockeye fisheries of the Skeena and Fraser systems. Because this outcome appears most closely related to habitat protection and stock development initiatives, these will be dealt with first. Development of fisheries regulations will be presented along with changes in catch and escapement patterns due to the profound effect of the latter two on the former.

HABITAT PROTECTION 1961–83

Two habitat protection issues served as dominant concerns of management and research personnel from the late 1950's to the early 1970's. These were: (i) a proposal for hydroelectric power development that would affect the Ash, Stamp, Sproat, and Somass rivers (Lash 1955), and (ii) continued expansion of the pulpmill at Port Alberni and the attendant impact of its effluent discharges on Alberni Inlet water quality, salmon rearing, and salmon migrations (Duncanson 1972).

The British Columbia Power and Electric Company proposed to build a series of dams to divert water from the Ash River and Great Central Lake through Sproat Lake to generate hydroelectric power. This posed two major threats to sockeye. First, large storage dams at the outlets of Great Central and Sproat lakes, along with dramatic alterations in seasonal and spatial patterns of discharge in rivers tributary to the Somass River, would threaten easy passage of sockeye to their spawning grounds. Second, the conversion of Great Central and Sproat lakes into storage reservoirs, with attendant increases in lake water level variations, had the potential to destroy most of the high quality spawning areas along alluvial fans and beaches. A wide range of studies were initiated by personnel of the Department of Fisheries, Fish Culture Development Branch to appraise the prospects for maintaining viable salmon stocks in the Somass system in the face of such developments. Before the studies could be completed, the power project was rejected in favour of the much larger hydroelectric power potential of the large rivers of the B.C. interior. This was fortunate for Barkley Sound sockeye conservation and stock development. Experience elsewhere (Mullan 1984; Stober and Tyler 1982) indicates that there has been limited success in overcoming the major problems such projects create for maintenance of salmon stocks.

The impact of deteriorating water quality on salmon, as a consequence of discharges of pulpmill effluent into Alberni Inlet, was potentially as serious and practically more immediate than that of hydroelectric development. The relationship between Somass River discharge and dissolved oxygen concentration developed in the 1940's by Tully (1949) had been used successfully for 20 yr to minimize adverse effects of pulpmill discharge on water quality and salmon in Alberni Inlet. However, through the 1960's and 1970's research revealed (Waldichuk 1965; Parker and Sibert 1972; additional references in Morris and Leaney 1980) that, given certain weather conditions, severe declines of oxygen levels could occur in the surface waters of Alberni Inlet such that the 5 $\mathrm{mg{\bullet}L^{-1}}$ of oxygen deemed as the acceptable minimum for salmonids (Alderdice and Brett 1957) would not be met.

Consultation between Federal Fisheries and the Provincial Waste Management Branch regarding this accumulated research resulted in an operating permit stipulating that effluent discharges associated with industrial expansion of the Port Alberni pulpmill were to be controlled such that dissolved oxygen levels above the halocline in the waters of Alberni Inlet were always in excess of 5 $\mathrm{mg{\bullet}L^{-1}}$. Consequently in 1965, MacMillan Bloedel began operating the storage dam, rebuilt in 1957 at the outlet of Great Central Lake, to provide water for mill effluent dilution in accordance with "rule curves" recommended by Department of Fisheries and Oceans engineers (Gordon 1965). In 1977, MacMillan Bloedel constructed and began operation of an aeration lagoon to reduce the biological oxygen demand of their effluent discharges. There is little doubt that Fisheries Department research and regulatory efforts have, in large part, been responsible for maintaining the viability of Alberni Inlet both for sockeye stock production and development.

Sockeye Stock Development 1961–83

The transformation of the Barkley Sound sockeye stocks into a major, sustained, commercial fishery has been accomplished through a remarkably successful yet informal set of interactions among fisheries management, fisheries research, and the sockeye themselves. Changes in the average production of the sockeye stocks appear in large part to be attributable to both research and enhancement initiatives involving lake fertilization and escapement optimization.

Lake Fertilization

From 1969 to 1975, investigators with the Fisheries Research Board of Canada conducted an experimental study at Great Central Lake (GCL) to test the hypothesis that increasing the supply of inorganic nutrients during the growing season in a highly oligotrophic lake would increase production at succeeding trophic levels and would consequently serve as a useful technique to enhance the productivity of a stock of sockeye salmon. LeBrasseur et al. (1978) reported that, during years of GCL fertilization (1970–73), mean summer primary production increased fivefold, zooplankton standing stock increased 9 times, the percentage survival from potential egg deposition to juvenile sockeye increased 2.6 times, and mean stock size of adult sockeye increased from less than 50 000 to greater than 360 000. The magnitude of the increase in adult returns was clearly unprecedented within the relatively short span (1958–75) of the GCL and Barkley Sound sockeye stock histories dealt with by these investigators (LeBrasseur et al. 1978; Manzer 1972, 1976) and is even more remarkable given the eighty plus years of quantified stock performance reviewed here (Fig. 3, 4, and 8).

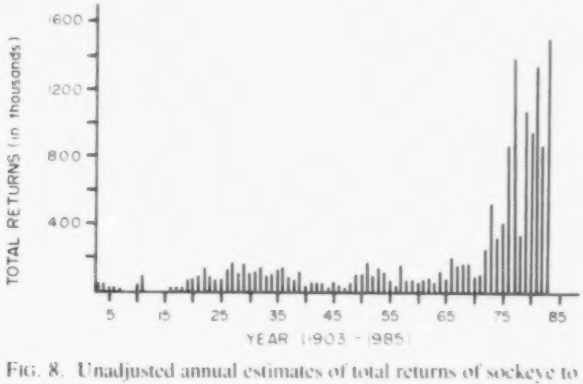

FIG. 8. Unadjusted annual estimates of total returns of sockeye to Barkley Sound between 1903 and 1983. Observations include: catch estimates only from 1903 to 1917, total catch plus Henderson escapement only from 1917 to 1926, total catch plus Henderson and Great Central escapements from 1926 to 1949, and total catch plus escapements to Henderson, Sproat, and Great Central lakes from 1950 to 1983.

There are many unanswered questions concerning the role of lake fertilization in promoting the increased returns of sockeye to GCL and in the intervening years many alternate hypotheses have been suggested as explanations for the increase. These range from coincidental solution of fish passage problems to elimination of water quality problems in Alberni Inlet or genetic adaptation of a recently established sockeye stock to a new lake environment. However, given the timing and nature of the events known to have affected the Barkley Sound sockeye stocks in general and the GCL stock in particular, a statement first made by LeBrasseur et al. (1978) is still germaine, i.e., "the substantial increase in Great Central Lake adult sockeye returns coincident with the fertilization program is of sufficient magnitude to render most difficult attempts to discount fertilization as the major causal factor."

Given the magnitude of the GCL stock increase in the years immediately after lake fertilization, LeBrasseur et al. (1979) concluded that lake fertilization could be utilized as a highly cost-effective technique to enhance sockeye salmon. Thus, when the Salmonid Enhancement Program (SEP) was launched in 1977 as a joint effort of the Federal and Province of British Columbia Governments, an expanded Lake Enrichment Program (LEP) was initiated by the Fisheries Research Branch (FRB) with funding provided by SEP. A wide range of additional coastal lakes are now under treatment (Hyatt and Stockner 1985) including both Henderson Lake (treatment initiated in 1976) and Sproat Lake (treatment initiated in 1985). Although it is too early to determine the precise impact of treatment on adult returns from these stocks, initial results for a number of them appear encouraging and apparent increases in recent years at Henderson Lake (Fig. 4a) in particular require closer examination.

Escapement Optimization

Although we acknowledge the role of lake fertilization in increasing the productivity of the GCL sockeye stock, it does not currently act alone to maintain the increased Barkley Sound sockeye production. Our research has demonstrated that with treatment, GCL can support juvenile populations from escapements far in excess of those which were routinely permitted prior to, or in the early years of fertilization. As recently as the late 1970's, GCL escapements of 50 000 adults were considered adequate. However, we have been unable to detect any decline in juvenile sockeye production even at escapements as high as 225 000 to 350 000 adults (Fig. 9). Untreated Sproat Lake also appears to have been chronically "underescaped", whereas the Henderson stock appears to have been both "overescaped" (early 1920's, Fig. 4a) and "underescaped" (early 1940's, mid 1970's) (Hyatt et al., unpublished data). These observations alone have contributed to the production of hundreds of thousands of additional Barkley Sound sockeye in recent years.

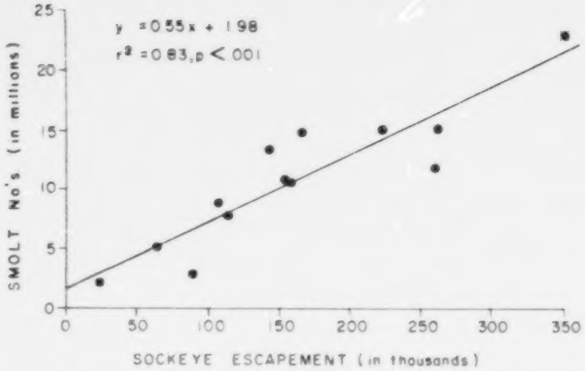

FIG. 9. Relationship between variations in brood-year escapement and resultant "smolt" production by Great Central Lake sockeye, 1970–82. Annual estimates of sockeye escapement were obtained through either visual (1970–74) or continuous electronic counts (1975–82) of adult sockeye passing through fishways. Estimates of annual variations in smolt production have been based on late summer to early winter census of juvenile sockeye via hydroacoustic and midwater trawling techniques (see Hyatt et al. 1984; Hyatt and Stockner 1985 for details).

CATCH, ESCAPEMENT, AND FISHERY REGULATIONS PATTERNS 1961–83

The massive increases in sockeye returns to Barkley Sound beginning in the early 1970's have profoundly changed the nature of the fishery with respect to (i) fishing vessel numbers, (ii) gear type, (iii) regulations employed to ensure orderly exploitation of the stocks, and (iv) the role that research plays in developing new management tools.

Given the large surplus of fishing fleet capacity that existed on the B.C. coast by the early 1970's, it is not surprising that, as large returns of sockeye materialized in Barkley Sound, there was a dramatic increase in the maximum number of fishing vessels that chose to participate in the fishery (Fig. 6). Although changes in Barkley Sound sockeye abundance were generally followed by rapid adjustments in fleet size during both the 1950's (Fig. 7a and b) and from 1961 on (Fig. 10a and b), there were two notable differences in the patterns of fleet response in the two intervals. The first difference was the much larger response from 1961 on, when as many as 350 gillnetters participated in the fishery. The second difference was that the fleet response to variations in fish abundance during the interval centered about the 1950's had been continuous and linear (gillnet vessels = 1.28 catch + 0.34, $r^2 = 0.86$, $P < .001$), whereas, more of the variation in gillnet vessel numbers observed during the 1960's and beyond is explained by a curvilinear model (log no. of vessels = 0.77 log catch + 0.23, $r^2 = 0.87$, $P < .001$ Fig. 10a) than by a strictly linear one (gillnet vessels = 0.27 catch + 37.77, $r^2 = 0.72$, $P < .001$). The tendency for fleet size to have levelled off in Barkley Sound during the latter interval may be a consequence of either fully utilized fishing space in Barkley Sound and Alberni Inlet, or depletion of much of its surplus capacity.

Fleet changes during the 1960's and 1970's were not restricted only to number of vessels participating. A shift toward vessel diversification also occurred as purse seiners were first allowed sporadic entry and finally, in the early 1970's, routine access to the sockeye fishery. This entry is well reflected as a decline in the proportion of the sockeye catch obtained by gillnetters between 1956 and 1984 (Fig. 11). The non-gillnet catch is largely taken by purse seiners, but minor quantities are taken by trollers and sport fishermen.

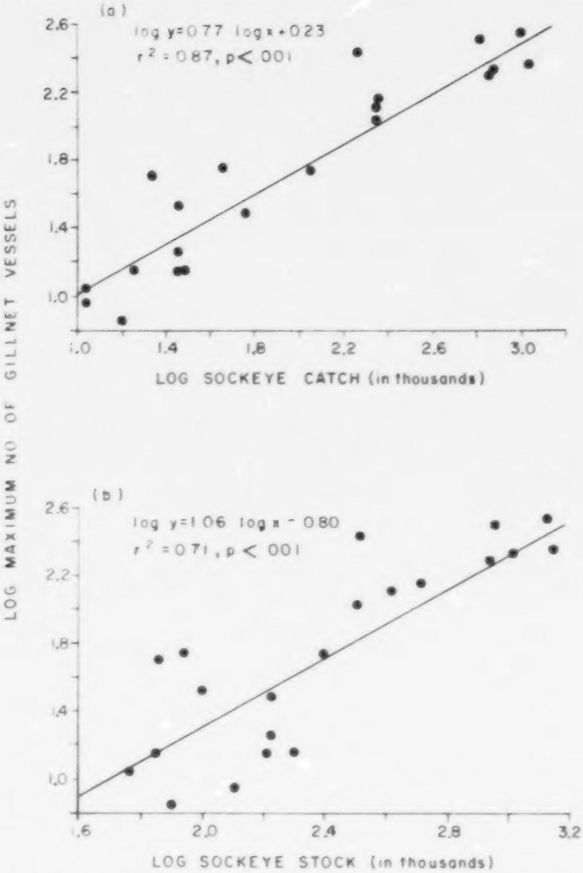

FIG. 10. Relationships between annual variations in the maximum number of gillnet vessels participating in the fishery and annual variations in sockeye abundance as indexed by (a) catch or (b) total returns between 1961–82. Note log scale on axis.

During the late 1950's and early 1960's, fisheries managers regulated Barkley Sound and Alberni Inlet net fisheries (principally gillnet) to focus exploitation on the sockeye returning to Henderson Lake while attempting to protect Somass stocks (Sproat and GCL) to build escapements. Subarea boundary changes within season were manipulated principally to open Uchucklesit Inlet and the subareas proximal to it (e.g., area, 23.3, Fig. 1) during the interval (late June to mid-August) when Henderson fish were known to arrive. At the same time, the upper end of Alberni Inlet (Chup or Pocahontas point to Somass River mouth) was often closed (Hyatt and Raymond, unpublished data).

The years 1969–71 marked a transition in subarea regulation during which the intent was to spread exploitation equitably across the Henderson and Somass sockeye stocks as all escapements appeared to need some protection (Fig. 4a, b, and c). During the fishing season of 1972, and in associa-

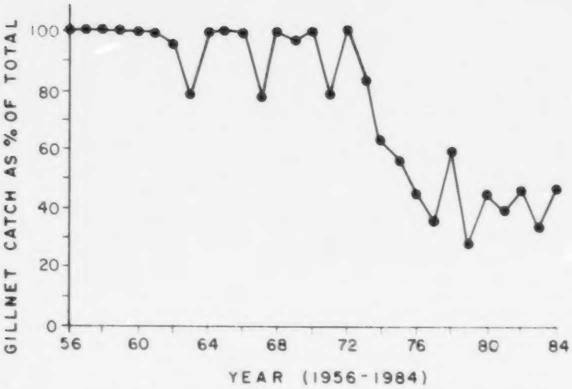

FIG. 11. Historical trend in the proportion (as %) of the total sockeye catch obtained by gillnet in each year between 1956 and 1984. The majority of catch not taken by gillnet is obtained by purse seine. A minor but increasing fraction (<5%) of the sockeye catch has been obtained by trollers and sports fishermen since the late 1960's.

tion with unusually strong returns of sockeye to the Somass, the landward boundary of the fishery within Alberni Inlet was progressively moved from Pocahontas Point (May 14), to Dunsmuir Point (July 2), to Polly Point (July 13) to enable the net fishery to harvest predominantly Somass sockeye (Fig. 1).

In the years since 1972-73, sockeye fishery regulations have shown the following general trends: Regulations are focused on the orderly exploitation by net fisheries of the large returns of sockeye to the Somass River; Subarea boundary changes are used within season to protect the Henderson escapement from exploitation in Uchucklesit Inlet; Subarea openings and closures within the fishing season are more frequent than in past intervals (4-5 sets of announcements per season), and are increasingly associated with the evolution of separate gillnet and purse seine fisheries as distinct from a common net fishery.

Fisheries research, which contributed so effectively toward protecting and developing the stocks historically, is now applied more often to development of new stock management tools. Evidence presented throughout this paper suggests that there have been a number of significant changes in the relative productivities of the three Barkley Sound sockeye stocks, and in their contributions to the mixed stock fishery. As these changes occurred there has been a constant risk that one or more of the Barkley Sound stocks would decline in the face of a fishery focused primarily on the most productive stock. This risk has been especially acute during the latest stock increase episode when the fishery spread through most of the waters of Barkley Sound and Alberni Inlet making mixed stock interceptions inevitable and stock identification increasingly difficult. However, this problem has been greatly reduced by development of tissue assays which have made it possible to identify stock specific parasite combinations (L. Margolis, unpublished data) and routinely partition the Barkley Sound catch according to stock of origin (Steer et al. 1986). The technique has been especially useful for refining current in-season management procedures to protect the Henderson sockeye stock which in recent years appears to have contributed less than 6% of the total catch (Table 3). This stands in sharp contrast to its performance during the late 1920's and 30's (Table 3) as well as that loosely documented over most of the course of the past 100 years of the Barkley Sound fishery.

Dedication

The more than a century of conservation and development of the Barkley Sound sockeye stocks, and the development and regulation of the associated sockeye fisheries surely stands as one of the more remarkable demonstrations of successful stewardship of a salmon resource by Canada's Department of Fisheries and Oceans. The quantitative changes during the last 80 years are nothing short of spectacular (Fig. 8 and Table 4). These changes have been no accident, but won through the efforts of 3-4 generations of dedicated fisheries managers and researchers who have often laboured in the face of great uncertainty and difficult odds to either prevent the deterioration of the stocks or to develop them further as circumstances permitted. Many of those involved have not survived to witness the rewards reaped by the present generation. This paper is dedicated first to these pioneers of the past, next to those who continue to labour in the present, and finally to those who will be entrusted with this precious resource in the future.

TABLE 4. Summary of catch associated with the Barkley Sound sockeye fishery by historical interval.

Interval	Mean catch (thousands)	Range of catch (thousands)
1860-1900	unknown	possibly 30- 50
1901-1920	29	5- 95
1921-1940	45	3- 125
1941-1960	28	5- 76
1961-1983	290	11-1 100

Acknowledgements

The idea for this paper emerged from discussions with the late Fred Withler. Both Fred and Vic Aro generously permitted us access to their files of unpublished documents pertaining to the history of Barkley Sound sockeye. Don McCulloch and Dennis Girodat of the District Fisheries Office in Port Alberni exhibited good natured tolerance of the many intrusions to comb their files for unpublished reports and they were instrumental in the recovery of much of the unpublished catch and escapement data. Thanks is also extended to Fay Winters, Bev Raymond, and James Radziul who aided in the assembly and analysis of historical observations concerning changes in the Native food fishery, fishery regulations, and sockeye passage problems, respectively.

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Catches of North American Sockeye Salmon (*Oncorhynchus nerka*) by the Japanese High Seas Salmon Fisheries, 1972–84[1]

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Abstract

HARRIS, C. K. 1987. Catches of North American sockeye salmon (*Oncorhynchus nerka*) by the Japanese high seas salmon fisheries, 1972–84, p. 458–479. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

A major change in the level and pattern of fishing by the Japanese high seas salmon fisheries in the North Pacific Ocean and Bering Sea occurred in 1977–78 as a result of revisions of the International Convention for the High Seas Fisheries of the North Pacific Ocean (North Pacific Treaty; Canada–Japan–USA) and the USSR–Japan Treaty. This paper examines the sockeye salmon catches and temporal and spatial distribution of fishing effort by the Japanese mothership and landbased driftnet salmon fisheries before and after 1977, and assesses how the regulatory measures imposed by the revised treaties have changed the level of high seas catch of North American sockeye. Information on the regional stock origins of immature and maturing sockeye in the past and present fishing areas is used to obtain estimates of stock composition of the high seas catches. The fisheries have caught mostly Asian fish, but substantial numbers of western Alaskan and some central Alaskan sockeye have also been caught. Catches by the mothership fishery of maturing sockeye after 1977 have averaged 885 000 fish, about one-half of the 1972–76 level, and the reduction is due largely to prohibition of May fishing imposed by the North Pacific Treaty revision. The mean proportion of Alaskan fish in the catches of maturing fish decreased little, from about 36% in 1972–76 to 28% in 1978–84. The mothership catches of immatures markedly increased in recent years because of heavy concentration of late-season fishing south of the western Aleutian Islands. The mean proportion of Alaskan fish in the catches of immatures decreased from 50% to 36%, but because of larger catches the number of Alaskan immature fish caught increased after 1977. Although exclusion of the sector southeast of 56°N, 175°E had a major effect in reducing potential mothership catches of Alaskan sockeye, the proportion of Alaskan fish in the catches declined surprisingly little because of the offsetting effect of area closures by the USSR–Japan agreements. Closure of the area east of 175°E in the landbased fishery area had little effect on the proportion of Alaskan fish in the catch, as the majority of the sockeye catch was always made west of 175°E. The catches of Alaskan fish by the landbased fishery greatly declined, however, mainly due to the changes imposed by the USSR–Japan Treaty.

Résumé

HARRIS, C. K. 1987. Catches of North American sockeye salmon (*Oncorhynchus nerka*) by the Japanese high seas salmon fisheries, 1972–84, p. 458–479. *In* H. D. Smith, L. Margolis, and C. C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Au cours de la saison de pêche de 1977–1978, on a vu un important changement de l'intensité et du régime des pêches hauturières japonaises du saumon dans l'océan Pacifique Nord et la mer de Béring à la suite des révisions de la Convention internationale sur les pêcheries hauturières de l'océan Pacifique Nord (Traité du Pacifique Nord: Canada–Japon–É.-U.) et du traité entre la Russie et le Japon. Dans le présent document, on examine les prises de saumon nerka et les distributions temporelles et spatiales de l'effort de pêche déployé par le bateau-mère japonais et les pêcheries au filet dérivant basées à terre avant et après 1977; de plus, on évalue comment les mesures de réglementation imposées par les traités révisés ont changé le niveau des prises hauturières de saumon nerka nord-américain. Des données sur les origines des stocks régionaux de saumon nerka immature et en maturation présents dans les pêcheries passées et actuelles sont utilisées pour obtenir des estimations de la composition par stock des prises hauturières. On y retrouve surtout des poissons d'origine asiatique, mais des nombres importants de saumons provenant de l'ouest de l'Alaska et une certaine quantité provenant du centre de l'Alaska ont aussi été capturés. Après 1977, les prises de saumon nerka en maturation au cours de la pêche par flottille et bateau-mère

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ont atteint en moyenne 885 000 poissons, soit environ la moitié des prises observées de 1972 à 1976; cette baisse est due en grande partie à l'interdiction de la pêche en mai imposée après la révision du Traité du Pacifique Nord. La proportion moyenne de poissons de l'Alaska dans les prises de saumon en maturation est passée d'environ 36 % en 1972–1976 à 28 % en 1978–1984. Les prises par bateau-mère de saumon immature ont nettement augmenté au cours des dernières années à cause d'une forte concentration de l'effort de pêche vers la fin de la saison au sud des îles Aléoutiennes ouest. La proportion moyenne de saumon de l'Alaska dans les prises de saumon immature est passée de 50 % à 36 % mais à cause de prises importantes, le nombre de saumon immature de l'Alaska a augmenté après 1977. Quoique l'exclusion du secteur au sud-est du 56°N, 175°E ait eu une incidence importante pour ce qui est d'une baisse des prises potentielles de saumon nerka de l'Alaska par flottille et bateau-mère, la proportion de poisson de l'Alaska dans les prises a étonnamment peu baissé à cause de l'effet compensatoire qu'ont eu les fermetures de zones à la suite des accords entre la Russie et le Japon. La fermeture de la zone à l'est du 175°E à la pêche basée à terre a eu peu d'incidence sur la proportion de poisson de l'Alaska dans les prises car la plus grande partie de celles-ci étaient toujours effectuées à l'ouest du 175°E. Toutefois, les prises de poisson de l'Alaska au cours de la pêche basée à terre ont fortement baissé principalement à cause des modifications imposées par le traité entre la Russie et le Japon.

Introduction

In 1952 Japan began two large high seas drift gillnet fisheries for salmon: a mothership fishery that has operated north of 46°N; and a landbased driftnet fishery that has operated mostly south of 46°N. These fisheries have been regulated to some extent by two international treaties, the International Convention for the High Seas Fisheries of the North Pacific Ocean (North Pacific Treaty, formed in 1952 between Japan, Canada, and the United States), and the USSR–Japan Treaty Concerning the High Seas Fisheries of the Northwest Pacific Ocean (USSR–Japan Treaty, formed in 1956). For the first 26 years the North Pacific Treaty regulated the high seas salmon fisheries mainly by setting their eastern boundary at a provisional line at about 175°W, but negotiations under the USSR–Japan Treaty have led to far more numerous and diverse regulations.

The North Pacific Treaty established the International North Pacific Fisheries Commission (INPFC), in part to recommend and review research required of member nations to serve as a basis for considering conservation measures for North American fish and shellfish stocks. INPFC-related high seas salmon research began in 1955, and by the late 1950's tagging experiments had already shown that Bristol Bay sockeye salmon migrate considerably west of 175°W, and were caught in large numbers by the new mothership fishery (see research summaries in late 1950's and early 1960's INPFC Annual Reports).

From the mid-1950's through 1976 the mothership and landbased fisheries made large catches across a broad area of the North Pacific and Bering Sea to 175°W, but in 1977–78, major changes in the North Pacific Treaty and USSR–Japan Treaty drastically reduced the authorized areas for the fisheries. In addition, recent USSR–Japan agreements have greatly reduced the catch quotas of the fisheries. These changes necessitated a major reduction in the size of the fisheries and a concomitant reduction of total fishing effort and catch. My aim in this paper is to assess how these recent changes in the Japanese high seas salmon fisheries have in turn changed the levels of catch of North American sockeye salmon.

Fredin and Worlund (1974) developed a method for estimating the mothership fishery's catches of Bristol Bay sockeye, and their general method has been used subsequently to update these estimates with each year's catch. However, reconsideration of some early information and analysis of new information gained from recent INPFC research provide a basis for improving these estimates. Prior to 1978 there was virtually no information on origins of sockeye salmon in the area of the landbased driftnet fishery (southwest of 46°N, 175°W), but the 1978 North Pacific Treaty Protocol placed heavy research emphasis on this area. Sufficient information has recently been gained to permit quantitative

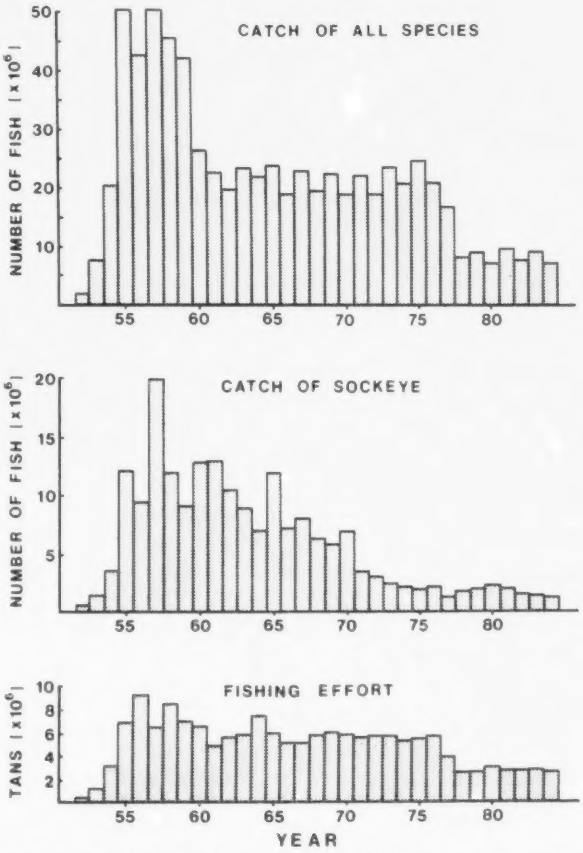

FIG. 1. Catch (in numbers of fish) and effort (in tans, gillnet segments about 45 m long) by the Japanese mothership salmon fishery in the North Pacific Ocean and Bering Sea, 1952–84. Source: INPFC (1979) and INPFC Documents.

estimates of the landbased fishery's catches of North American sockeye, as well.

The period 1972–84 was selected for this study for two reasons: (1) the mothership fishery's sockeye catches declined greatly to a new, less variable level beginning in 1971 (Fig. 1); and (2) Japan began to provide consistently detailed statistics for the landbased fishery in 1972. The closure of the USSR 200-mi zone and delay of fishing in 1977 resulted in a unique pattern of fishing, and therefore this paper will compare sockeye catches between 1972–76 and 1978–84.

History of the Fisheries and of Governing Treaties

Descriptions of the Japanese mothership and landbased driftnet fisheries were given by Moiseev (1956), Kasahara (1963, 1972), Chitwood (1969), Manzer et al. (1965), Taguchi (1966), Nagasaki (1967), Fukuhara (1955, 1971), and Fredin et al. (1977). The present description will entail only a brief review of the magnitudes of the fisheries and of international agreements affecting them.

Statistics for the mothership fishery can be found in INPFC Statistical Yearbooks, INPFC (1979), and Manzer et al. (1965). The mothership fishery developed rapidly, from two fleets in 1952 to a maximum of 16 fleets in 1956–59 (INPFC 1979). Total annual salmon catches (excluding those in the Okhotsk Sea in 1955–58) averaged 46 million in 1955–59 (Fig. 1). In 1960–76 catches were lower, at about 22 million fish annually. Since 1976, the mothership fishery has been reduced from 10 motherships in 1972–76 to four in 1978–84, and there has been a concomitant decrease in total fishing effort. Recent (1978–84) annual catches have averaged eight million fish.

The mothership fishery quickly began to exploit the sockeye salmon in the western Aleutian/Komandorskie region; its sockeye catches increased from an average of 1.9 million fish in 1952–54 to 9.8 million in 1955–70. The proportion of sockeye in the total salmon catch averaged 35.5% in 1952–70. After 1970, there was a marked decline in sockeye catches, to an average of 2.5 million annually in 1971–77 and 2.0 million annually in 1978–84. The mean proportion of sockeye in the total catches was 11.7% in 1971–77, but increased to 23.4% in 1978–84.

Two distinct fisheries engage in landbased driftnet fishing for salmon in the North Pacific (Japan Fisheries Agency, Tokyo, pers. comm.). One fishery consists of only small (under 10 gross tons) vessels that numbered about 1 200 in 1962–76 and 671 in 1984. This segment of the landbased fishery is not considered further in the present paper, as it has operated entirely west of 153°E (149°E before 1977), and its sockeye catches are negligible and likely do not include any fish of North American origin. The larger offshore landbased fishery has consisted of both small (under 30 gross tons) and larger vessels, but the small-vessel component ceased to exist after 1971. The large vessels increased in number from 58 in 1952 to a maximum of 374 in 1972–74, and decreased to 209 in 1978–84 (Japan Fisheries Agency, Tokyo, pers. comm.).

Catch statistics for the early offshore landbased fishery are difficult to extract from INPFC Statistical Yearbooks. Fredin et al. (1977) estimated the early catches, and the present report uses their catch figures except for 1962 and 1972–84, for which detailed statistics are available through the INPFC.

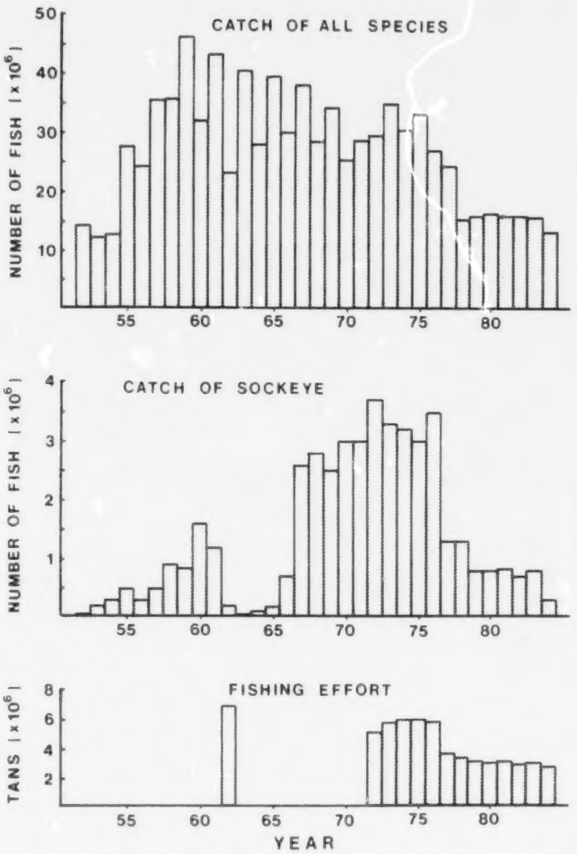

FIG. 2. Catch (in numbers of fish) and effort (in tans, gillnet segments about 45 m long) by the Japanese offshore landbased driftnet salmon fishery, 1952–84. Source: Fredin et al. (1977) for 1952–61, 1963–71; INPFC Documents for 1962, 1972–84.

The landbased fishery also developed quickly; the average total annual catch increased from 13 million fish in 1952–54 to 32 million in 1955–77 (Fig. 2). Following major reductions of the fishing area and fleet size in 1977 and 1978, total fishing effort decreased, and total salmon catches decreased to an average of 16 million fish in 1978–84. Sockeye catches were generally low (mean 0.5 million fish) in 1952–66. In about the late 1960's the large vessels began fishing farther eastward and sockeye catches increased, averaging 3.0 million in 1967–76. In 1977–84 the reduced fishery has caught an average of 0.9 million sockeye annually.

The North Pacific Treaty was signed in 1952, and was based on the abstention principle that grew out of U.S. fisheries policy of the 1930's and 1940's (Atkinson 1964; Johnson 1967; Yamamoto 1967; Taguchi 1966; Kasahara and Burke 1973; Hollick 1981; Jackson and Royce 1986). Virtually nothing was known about ocean distributions of North American and Asian salmon at the time of treaty negotiation, so a provisional eastern boundary for the new Japanese high seas salmon fisheries was set in an Annex under the treaty at about 175°W (175°W in the Bering Sea and about 175°20′W south of Atka Island; Fig. 3). No consensus was ever reached in many years of INPFC deliberations regarding the qualification of North American salmon stocks for

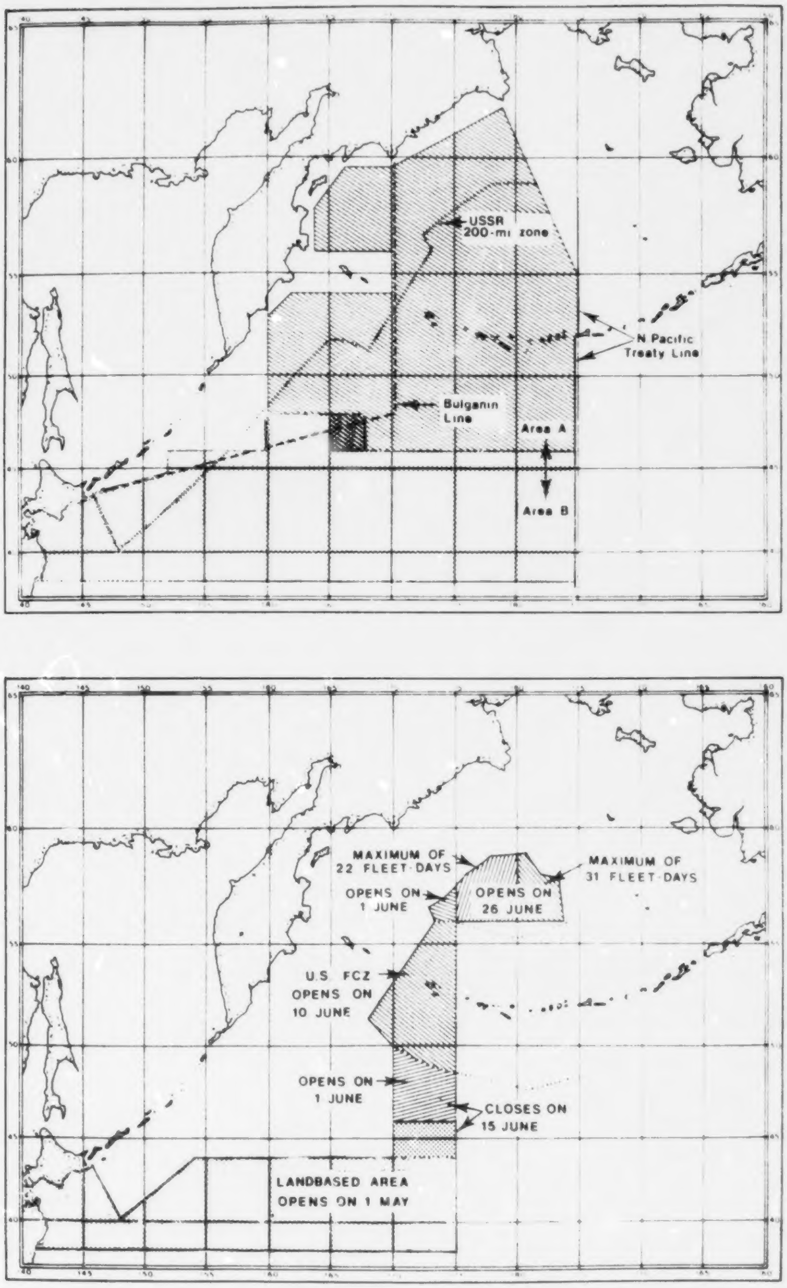
USSR 200-mi zone
N Pacific Treaty Line
Bulganin Line
Area A
Area B
MAXIMUM OF 22 FLEET-DAYS
MAXIMUM OF 31 FLEET-DAYS
OPENS ON 1 JUNE
OPENS ON 26 JUNE
U.S. FCZ OPENS ON 10 JUNE
OPENS ON 1 JUNE
CLOSES ON 15 JUNE
LANDBASED AREA OPENS ON 1 MAY

FIG. 3. Area of the Japanese mothership (crosshatched) and landbased driftnet (stippled) salmon fishery areas before 1977 (top panel) and after 1977 (bottom panel). The fishing area in 1977 was the same as shown in the top panel, except the USSR 200-mi zone was excluded. The 15 June closure of the area 170°E-175°E and between 46°N and the U.S. 200-mi zone (FCZ) first went into effect in 1979. Areas A&B, shown north and south of 45°N, respectively, in the upper panel were separate regulatory areas under the pre-1978 USSR-Japan Treaty.

abstention or regarding the appropriateness of the line at 175°W, so as a compromise the original treaty continued until 1978.

In 1977 the United States implemented the Magnuson Fishery Conservation and Management Act of 1976 (MFCMA), which established a 200-mi fishery conservation zone and claimed management authority over anadromous salmonids of U.S. origin throughout their migratory range (except where their range is within another country's fishery zone as recognized by the United States). The MFCMA also called for withdrawal from international agreements that could not be renegotiated to be brought into conformity with the terms of the new law. Renegotiation of the North Pacific Treaty took place in early 1978, and resulted in a revised Protocol and a new Annex that contained certain regulations for the Japanese high seas salmon fisheries. The new Annex closed the area southeast of 56°N, 175°E, prohibited the mothership fishery from operating before June, set fishing periods for various areas inside and outside the U.S. 200-mi zone, and limited the number of mothership fleet-days northeast of 56°N, 175°E (Fig. 3). Most of these new regulations were designed specifically to protect Bristol Bay sockeye salmon.

The USSR–Japan Treaty was negotiated in 1956, as a result of USSR concern about the new, rapidly growing high seas fisheries (Atkinson 1964; Taguchi 1966). A major function of the Soviet–Japan Fisheries Commission (SJFC), created by the treaty, has been the setting of annual catch quotas, but it has also regulated times and areas of operation, gear characteristics, and other aspects. The total high seas salmon catch quotas steadily declined from 120 000 t in 1957 to 80 000 t in 1976. A major blow to the fisheries came in 1977 when the USSR further reduced the quota (to 62 000 t) and closed the USSR 200-mi zone to high seas salmon fishing. In 1978, a revised USSR–Japan agreement closed the area northwest of 44°N, 170°E (except for a small section which is in the U.S. 200-mi zone), established a much more restrictive quota system, and obligated Japan to pay a cooperation fee to the USSR for the privilege of catching USSR-origin salmon on the high seas. The 1978–84 quotas were specified in terms of numbers of fish as well as in weight, and quotas were set for the total ocean harvest as well as for the "high seas" catches made outside of Japanese and U.S. 200-mi zones. The total salmon catch quotas have further declined, from 42 500 t in 1978 to 40 000 t in 1984. For the "high seas" area, there have also been separate species quotas. The sockeye quotas for the area seaward of 200-mi zones have been reduced from the initial 1.6 million fish in 1978 to 1.05 million fish in 1984 (various U.S. Embassy, Tokyo, communications).

International pressure resulted in some major restrictions and voluntary abstentions pertaining to sockeye salmon catches before the revisions of the treaties in 1977–78. For instance, the USSR had long been concerned about high seas interceptions of Kamchatkan sockeye (Moiseev 1956; Anon. 1962; Taguchi 1966; Selifonov 1975). The SJFC took several actions over the years to protect USSR sockeye, including the setting of sockeye quotas, certain time/area closures, and restrictions of fishing effort (Atkinson 1964; Fredin et al. 1977). Also, the United States had long expressed concern about the catch by the mothership fishery of Bristol Bay sockeye, and in bilateral talks Japan agreed to abstain from fishing in 1974–77 in certain times and areas to protect (mainly maturing) Bristol Bay fish.

Temporal and Spatial Distribution of High Seas Sockeye Catches

In this paper, data are compiled by month and 5°-longitude sub-area. Ten sub-areas were defined for the mothership fishery area by Fredin and Worlund (1974), and sub-areas 11–15 were defined for the landbased area by Myers et al. (1984) (Fig. 4). The landbased sub-areas subdivide only the area east of 160°E, because virtually all of the landbased sockeye catches have been made east of 160°E (1972–84 mean is 98.6%) and there is no evidence that North American sockeye occur west of 160°E.

Figure 5 shows the average temporal and spatial pattern of sockeye catch by the mothership fishery, relative to time/area allocation of fishing effort and relative to sockeye

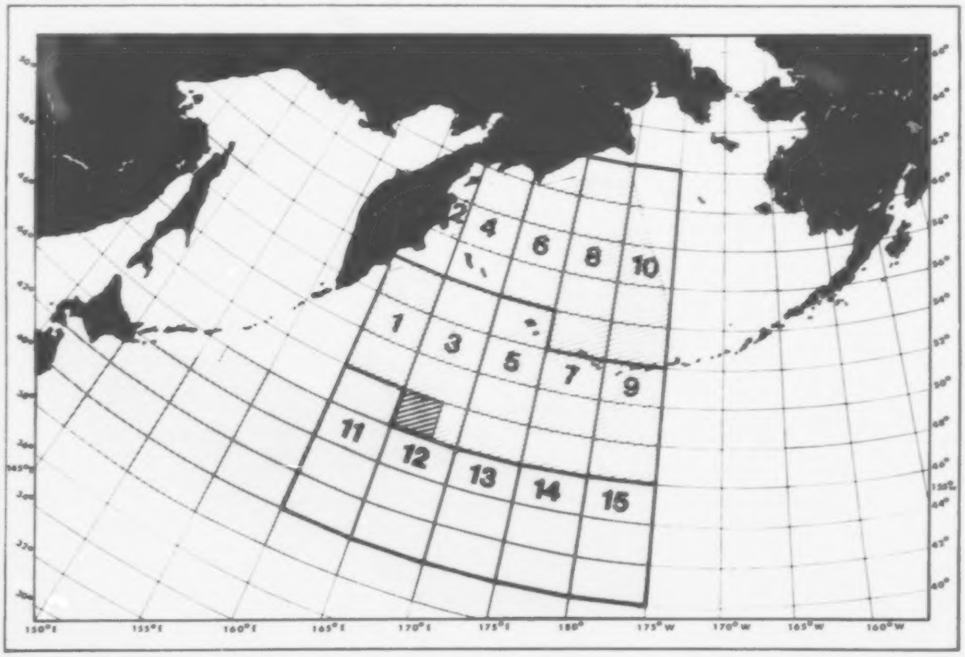

FIG. 4. The high seas salmon fishery area and statistical sub-areas used in this study. For the purpose of compiling landbased driftnet statistics, sub-area 12 is considered to extend north to 48°N.

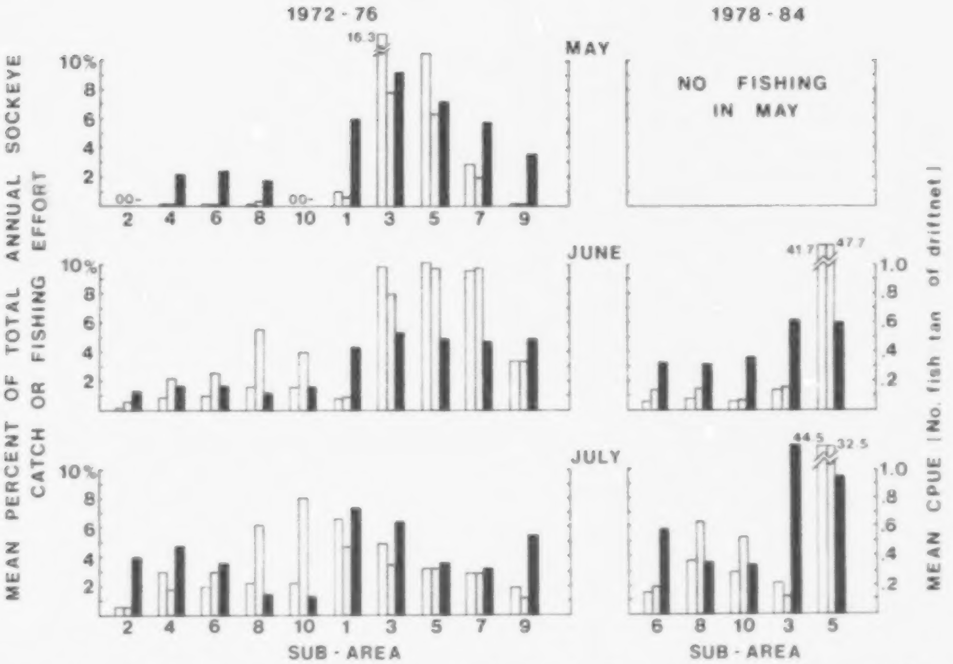

FIG. 5. Average spatial and temporal distribution of sockeye catch, effort, and sockeye catch per unit of effort by the Japanese mothership salmon fishery, 1972–76 and 1978–84. Open and crosshatched bars show the mean proportion of total annual sockeye catch and effort, respectively, in each sub-area/month stratum, and the solid bars show mean sockeye catch per tan of driftnet.

abundance. Values plotted are the mean proportions of total annual sockeye catch and of total annual effort, and mean catch per unit of effort (CPUE) in each month/sub-area stratum, for two periods, 1972–76 and 1978–84. CPUE is in terms of number of fish per tan (= about 45 m) of drift gillnet. The 1977 pattern of fishing was anomalous in several respects, and was therefore excluded from the calculation of period means. The U.S.–Japan governmental agreements of 1974–76 restricting fishing in certain times and areas to protect Bristol Bay sockeye did not result in greatly different allocations of effort between 1972–73 and 1974–76, at least when the statistics are compiled by month and sub-area, and therefore data for all 5 years 1972–76 were averaged to represent the early period.

Fishing in May 1972–76 was largely concentrated south of the Aleutian Islands in sub-areas 3, 5, and 7, where sockeye abundance was highest. In June, fishing was more dispersed, but areas of highest sockeye CPUE were still the most heavily fished. More fishing took place in the Bering Sea in June than in May, for the purpose of catching pink and especially chum salmon (Ito 1983). Sub-area 1 had fairly high sockeye abundance in May and June, yet was lightly fished because fishing was prohibited there (by USSR–Japan agreement) from 15 May through 25 June (in 1973–75) or through 30 June (in 1976). Even more fishing effort was expended in the Bering Sea in July (especially in sub-areas 8 and 10), but the next two most heavily fished sub-areas (1 and 3) had relatively high abundances of sockeye.

In 1978–84 the mothership fishery was permitted to operate only in June and July and in a much smaller area than in earlier years. In June, fishing was highly concentrated in sub-area 5, an area of relatively high sockeye abundance. Sub-area 3 had the highest mean sockeye CPUE, but only a small sector of sub-area 3 has remained in the 1978–84 fishery area (Fig. 4), and hence little effort was placed there. Bering Sea sub-areas 8 and 10 have been fished more heavily in July than in June (in part because these sub-areas have opened in the last week of June), but July fishing was heaviest in sub-area 5, where sockeye were abundant.

Statistics for the landbased driftnet fishery are similarly compiled in Fig. 6. Statistics for a small amount of out-of-area fishing in 1978–84 (in sub-areas 1, 3, 5, 7, and 14) were not included in the calculations. In May 1972–76 the vessels fished mostly in sub-areas 11–13, where sockeye CPUE was high. The distribution of effort was also influenced by some emphasis on fishing for pink and chum salmon, which tend to be in highest abundance somewhat west of the areas of highest sockeye abundance (Harris 1978). In June, fishing was heavily concentrated westward to target on pink salmon. Less fishing occurred in July, and it was again concentrated farther eastward for the purpose of catching coho salmon, which are most abundant in sub-areas 13–15 (Harris 1978).

In 1978–84, landbased fishing in May was heaviest in sub-areas 12 and 13 where sockeye CPUE was greatest. The overall CPUE of sockeye was lower than in 1972–76, because in 1978–84 the fishery was limited to south of 44°N (except in sub-area 13; see Fig. 3), close to the southern limit of sockeye distribution (French et al. 1976). In June, fishing was heaviest west of 160°E where pink salmon have been caught in greatest numbers, and also in sub-area 13 where coho are an important component of the catch. There was relatively little fishing in July, as the fishery has usually terminated operations in early or mid-July, after reaching its domestic allocation of the catch quota set by the SJFC.

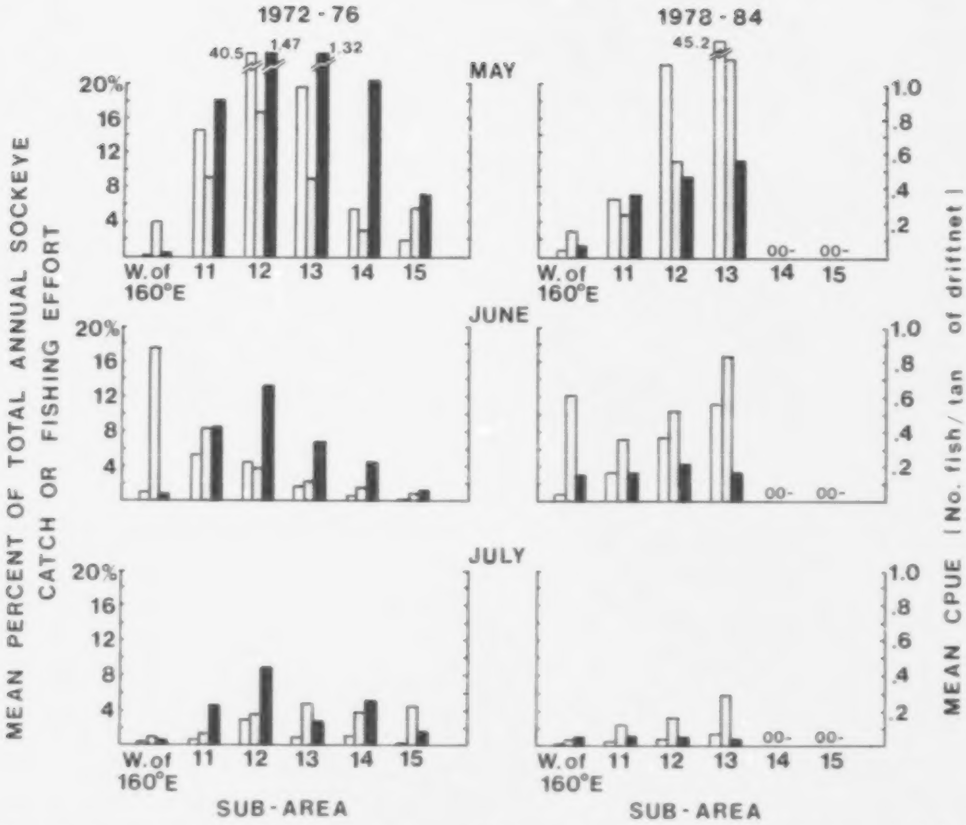

FIG. 6. Average spatial and temporal distribution of sockeye catch, effort, and sockeye catch per unit of effort by the Japanese landbased driftnet salmon fishery, 1972–76 and 1978–84. Open and crosshatched bars show the mean proportion of total annual sockeye catch and effort, respectively, in each sub-area/month stratum, and the solid bars show mean sockeye catch per tan of driftnet.

Sockeye abundance in July is very low, and likely did not greatly influence the fishing strategy.

Origins of Sockeye in the High Seas Fishery Area

Most of the information useful in estimating regional stock origins of sockeye in the western North Pacific and Bering Sea has come from INPFC-related tagging studies, an age composition analysis by Fredin and Worlund (1974), and, for the area south of 50°N, scale pattern analyses by Cook et al. (1981) and Knudsen and Harris (1982). Other studies based on scale analysis and on morphological and parasitological analyses provide additional information, and were summarized by French et al. (1976).

INFORMATION FROM TAGS AND PARASITES

The results of high seas tagging experiments by INPFC member nations in 1956–84 are valuable for qualitative studies of distribution, but they are of limited use in quantitative estimation of stock mixtures in the high seas population. The detection of region-specific parasite "tags" has provided information on the area of intermingling of Kamchatkan and Bristol Bay sockeye (Margolis 1963). The cestode parasite *Triaenophorus crassus* is present in sockeye of only Bristol Bay origin (with very rare exceptions), and the nematode *Dacnitis truttae* apparently occurs only in Kamchatkan sockeye. Data from parasitological analyses are also difficult to apply quantitatively. Margolis (1963) noted that *Dacnitis* is much less useful than *Triaenophorus* for determining the ocean distribution of its host sockeye stock-group. Unfortunately, the *Triaenophorus* infection rate is low for the Kvichak River stock, which is often the most abundant Bristol Bay stock.

Figures 7 and 8 show the monthly distributions of maturing and immature sockeye, respectively, from four major geographic regions, as indicated by tagging or parasite detection between 160°E and 170°W in May to July (the period of high seas fishing). The regional stock groups considered are: (1) Asia (essentially Kamchatka), (2) western Alaska (Arctic Alaska, Bristol Bay, north Alaska Peninsula, and Aleutian Islands), (3) central Alaska (south Alaska Peninsula to Bering River), and (4) southeast Alaska/British Columbia (Yakutat to Washington). The numbers of tags and parasites indicated in Fig. 7 and 8 for some sub-areas are less than shown in a similar figure prepared by Fredin and Worlund (1974), as Fig. 7 and 8 include data for just those months when the fisheries operated.

Tag and parasite data indicate that Asian and western Alaskan sockeye are represented in the population of maturing fish in May — Asian fish likely predominating in sub-areas 1 and 3 and extending to sub-area 9, and western

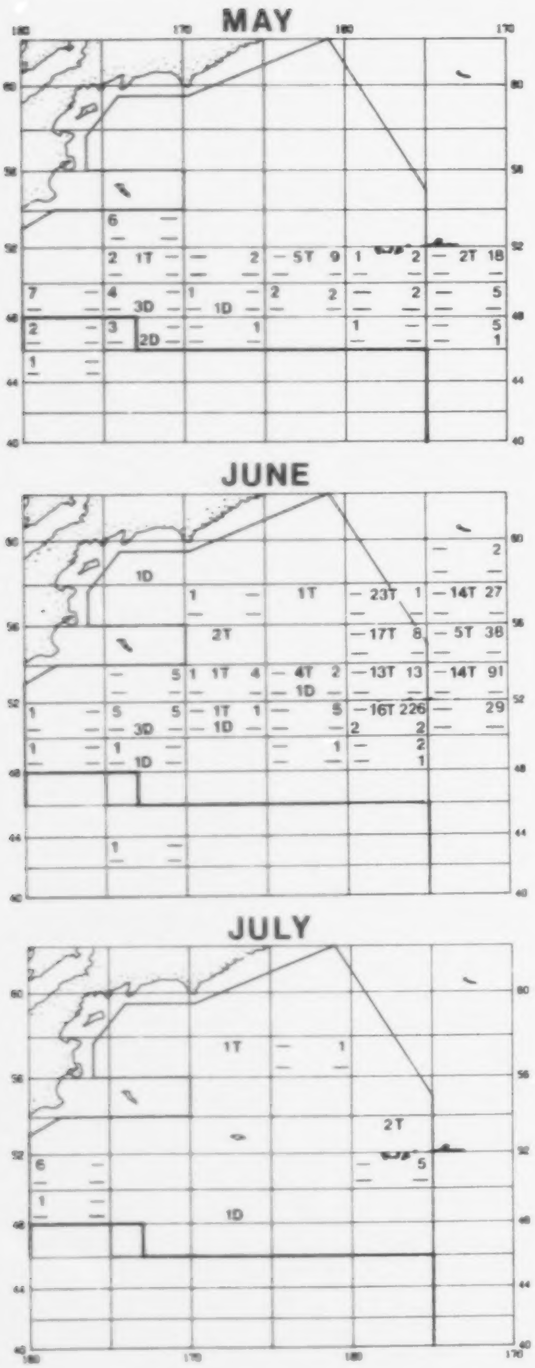

FIG. 7. Summarized results of 1956–84 INPFC tagging of maturing sockeye, and of parasitological study of maturing sockeye. The numbers of coastal recoveries from releases of maturing sockeye in each 2° × 5° statistical area from Asia, western Alaska, central Alaska and southeast Alaska/British Columbia (including Washington) are shown in the NW, NE, SW and SE corners of each statistical area, respectively. The number preceding "T" in the middle of an area is the number of *Triaenophorus*-infected (i.e., Bristol Bay) fish detected, and the number preceding "D" is the number of *Dacnitis*-infected (i.e., Kamchatkan) fish detected; information on parasites was compiled from Margolis (1963).

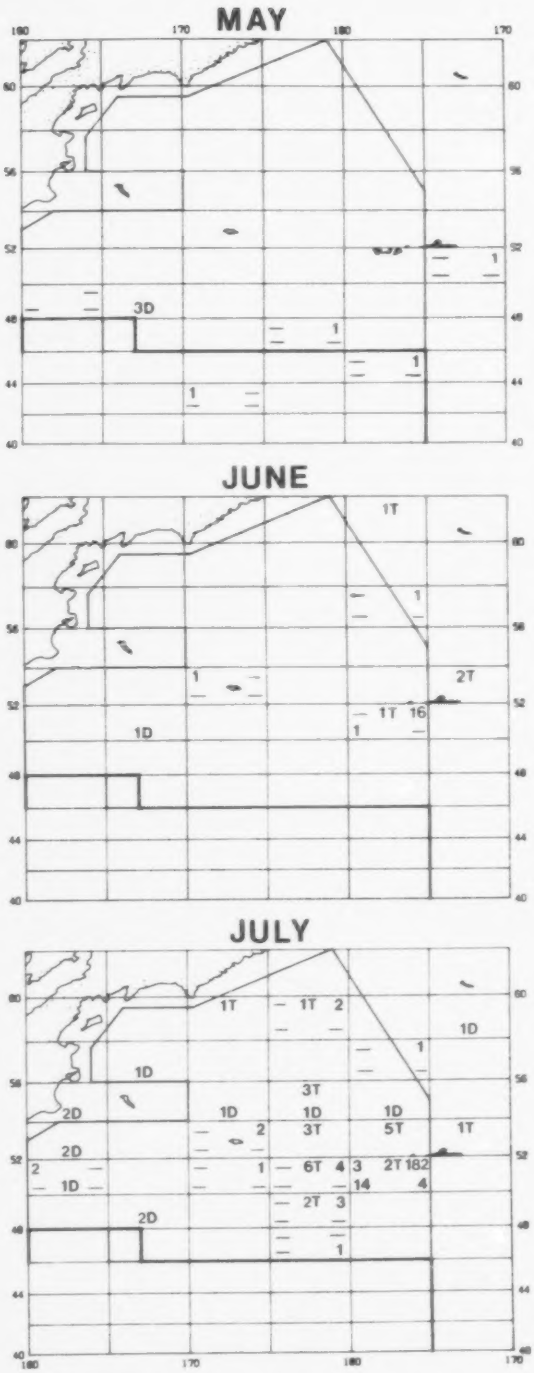

FIG. 8. Summarized results of 1956–84 INPFC tagging of immature sockeye, and of parasitological study of immature sockeye. The numbers of coastal recoveries from releases of immature sockeye in each 2° × 5° statistical area from Asia, western Alaska, central Alaska and southeast Alaska/British Columbia (including Washington) are shown in the NW, NE, SW and SE corners of each statistical area, respectively. The number preceding "T" in the middle of an area is the number of *Triaenophorus*-infected (i.e., Bristol Bay) fish detected, and the number preceding "D" is the number of *Dacnitis*-infected (i.e., Kamchatkan) fish detected; information on parasites was compiled from Margolis (1963).

Alaskan fish likely predominating in sub-areas 7 and 9 and extending westward to sub-area 3. In June, maturing western Alaskan fish clearly extend to sub-area 3, and central and southeast Alaska/B.C. fish occur in sub-area 9. Maturing Asian fish are indicated to occur eastward as far as sub-areas 5 and 8 in June. There are many fewer recoveries for maturing fish tagged in July. Intermingling of Asian and western Alaskan fish is still evident in July in the sub-area 5–6 sector of the mothership fishery area. There are few tag recoveries available from May–July releases of maturing fish in the landbased area, and they are all from Asia. The occurrence of maturing western Alaskan and southeast Alaska/B.C. fish in the vicinity of the area is indicated by tagging data, however (Fig. 7).

There are few tag recoveries available for immature fish in May, but they indicate occurrence of Asian fish in the mothership and landbased fishery areas west of 175°E and occurrence of western Alaskan fish east of 175°E (Fig. 8). In June, the same general pattern is true for the mothership area, and immature central Alaskan fish are found in sub-area 9. For July, tag recoveries and incidence of parasites indicate occurrence of Asian immatures far to the east, and western Alaskan fish extend to sub-areas 5 and 6. The occurrence of central Alaskan immatures in sub-area 9 in July is well indicated, and southeast Alaska/B.C. fish extend as far west as southern sub-area 7.

AGE COMPOSITION ANALYSIS

Fredin and Worlund (1974) estimated the proportions of Kamchatkan and Bristol Bay maturing and immature sockeye in the mothership area in 1956–70 by a complex method employing tagging and parasitological data and data on migratory speed and age composition. They did not have information on the maturity composition of mothership catches, and were forced to devise a scheme based on time/area stratification for breaking the important ocean age[2] .2 group into maturing and immature components. Also, after examining tagging and parasitological data, they made the assumption that sockeye west of 170°E are entirely of Asian origin, that maturing sockeye east of 175°E through late June are entirely of Bristol Bay origin, and that immature fish in sub-areas 7 and 9 after 20 June are entirely of Bristol Bay origin. Thus, intermingling of Asian and Bristol Bay fish was assumed to occur only in sub-areas 5 and 6 for maturing fish and sub-areas 5, 6, 8, and 10 for immatures (Fig. 9). The fraction of North American fish from areas other than Bristol Bay was thought to be very small, and was ignored in the classification procedure.

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[2] Age is designated such that the number of ocean annuli on the scale follows the period, and the number of freshwater annuli precedes it.

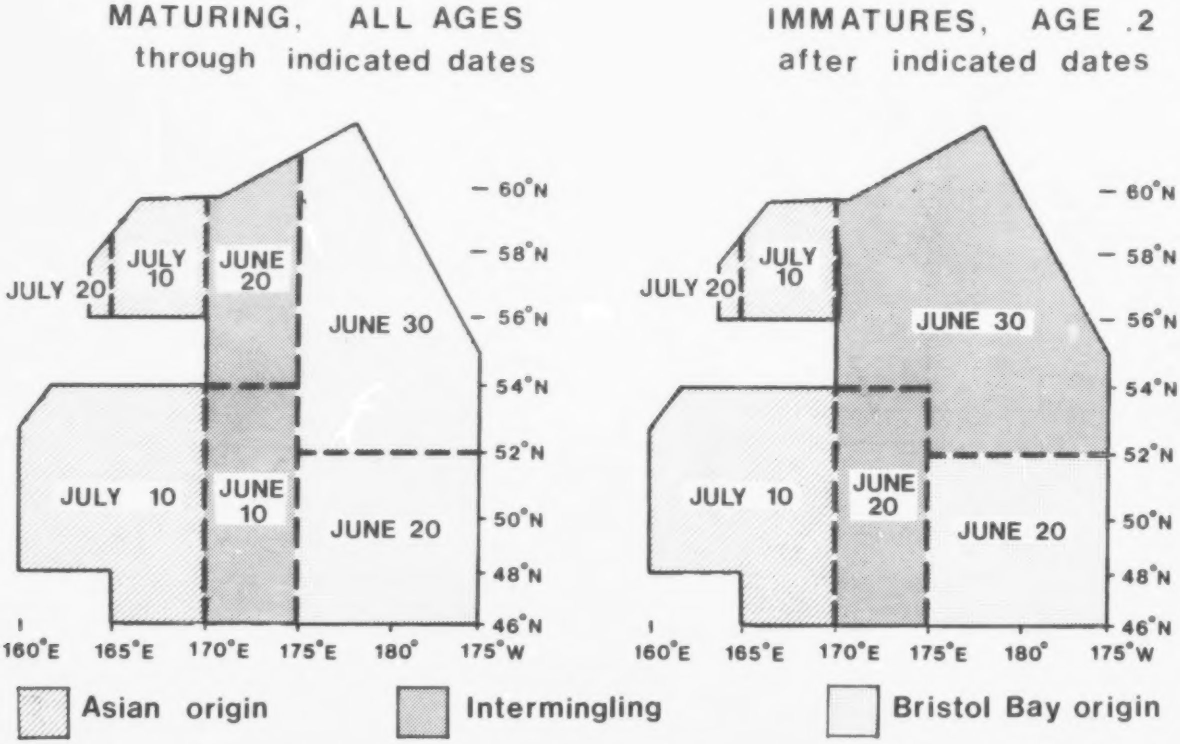

FIG. 9. Schematic summary of assumptions made by Fredin and Worlund (1974) regarding maturity composition of age .2 sockeye and regarding origins of sockeye in the area of the Japanese mothership salmon fishery. (See Fredin and Worlund, 1974 for the full set of their assumptions.)

For the areas of assumed intermingling, Fredin and Worlund (1974) calculated the most likely combination of the two stock-groups that provided the age composition obtained from sampling on motherships. For this procedure, Asian and Bristol Bay "standard" age compositions were determined on the basis of samples from the areas assumed to have exclusively Asian or Bristol Bay fish. Estimates of the proportion of Bristol Bay fish in the 1960–70 mothership catches of maturing fish in sub-areas 5 and 6 ranged from 6% to 80% and averaged 42%. Estimates for Bristol Bay immatures in sub-areas 5, 6, 8, and 10 were from 1% to 92% and averaged 37%.

The overall classification method used by Fredin and Worlund (1974) is clearly based on a series of assumptions. Perhaps the two most contestable assumptions, which will be discussed later, are the scheme used to estimate maturity composition of age .2 fish, and the designation of various sub-areas populated exclusively by Asian or Bristol Bay fish.

SCALE PATTERN ANALYSIS OF SOCKEYE SAMPLED SOUTH OF 50°N

Cook et al. (1981) and Knudsen and Harris (1982) applied scale pattern recognition techniques to estimate the regional stock composition of the sockeye population in the landbased fishery area, using samples collected south of 50°N and between 160°E and 175°W in May and June, 1972–76. The analysis was stratified by age and maturity group (ages 1.2, 2.2, 1.3, and 2.3 maturing fish and ages 1.2 and 2.2 immatures, the principal age/maturity groups in driftnet catches). The original analysis by Cook et al. (1981) employed standard samples representing Asian, western Alaskan, and central Alaskan stock-groups, but as that analysis was being completed, new tag recoveries suggested that southeast Alaska/B.C. fish may also occur in the landbased fishery area. Knudsen and Harris (1982) then repeated the analysis for age 1.2 maturing fish (the predominant age group in the southeast Alaska/B.C. region) employing an additional category representing that region.

Because these studies did not report estimated stock proportions by sub-areas as defined in Fig. 4, I used Cook et al.'s (1981) classification results to make new, corrected estimates for sub-area/month strata. Cook et al.'s results were used even for the age 1.2 maturing group, as Knudsen and Harris (1982) obtained very low and consistently nonsignificant estimates of contribution by the southeast Alaska/B.C. stock-group. Unweighted means of the new estimates for all age-groups and years are presented in Table 1A. Table 1B provides similar unweighted mean estimates for maturing fish for times and areas in which Fredin and Worlund (1974) assumed all fish are maturing; sample sizes in the classification results did not permit estimation of stock composition for immature fish after Fredin and Worlund's assumption dates. Although Table 1B is provided as a basis for comparing stock composition estimates from the scale study and from the analysis by Fredin and Worlund (1974), only a coarse comparison is justified because of major procedural differences between the two studies.

Table 1A shows that the average estimated stock proportion for Bristol Bay maturing fish is highest in the eastern sub-areas and declines greatly to the west. The suggested relative contribution of Asian fish in sub-areas 7 and 9 is considerably higher in both May and June than is suggested by tagging results or by Fredin and Worlund's (1974) study. Estimated contribution of central Alaskan maturing sockeye is generally low; the high average proportion (20%) in sub-area 1 in May (Table 1A) was caused by some individual estimates that are suspected to be spurious (Harris et al. 1982; Cook 1982). When estimates were calculated for longer time periods (Table 1B), the estimated proportion of central Alaskan fish in sub-area 1 is lowered, and the east-west gradients of relative contribution of Bristol Bay and Asian fish are readily seen. The mean estimated proportion of Bristol Bay maturing fish in sub-area 5 through June 10 is 32%. In comparison, 46% is the corresponding mean of 1960–77 estimates obtained for the same time/area stratum by the method of Fredin and Worlund. A generally similar spatial trend is seen in Table 1A for immature fish. There is again

TABLE 1. Unweighted means of stock-group composition estimates, based on classification results of Cook et al. (1981). Estimates were averaged over all years and age-groups represented in each combination of maturity group and sub-area/period stratum.

Part A: Means of estimates calculated for sub-area/month strata

Maturity group	Month	Sub-area	No. of estimates averaged	Mean % composition		
				Bristol Bay	Central Alaska	Kamchatka
Maturing	May	1	7	6	20	74
		3	16	11	4	85
		5	10	30	4	66
		7	9	31	14	55
		9	5	68	10	22
		11	12	5	7	88
		12	9	5	4	91
		13	2	6	3	91
Maturing	June	1	7	5	3	92
		3	9	7	6	87
		5	3	13	6	81
		7	1	49	9	42
		9	4	74	3	23
		11	4	9	7	84
		12	4	8	2	90

TABLE 1. (*Continued.*)

Part A: Means of estimates calculated for sub-area/month strata

Maturity group	Month	Sub-area	No. of estimates averaged	Mean % composition		
				Bristol Bay	Central Alaska	Kamchatka
Immatures	May	5	3	11	6	83
		11	4	7	5	88
		12	3	8	1	91
		13	2	14	0	86
		14	2	23	8	69
Immatures	June	3	3	18	0	82
		5	4	22	3	75
		7	5	31	12	57
		9	4	50	20	30
		11	1	8	0	92
		12	3	4	2	94
		13	2	8	19	73

Part B: Means of estimates for sub-areas 1, 3, 5, 7 and 9 calculated for maturing fish in time period through Fredin and Worlund's (1974) assumption dates.

Sub-area	Through indicated date	No. of estimates averaged	Mean % composition		
			Bristol Bay	Central Alaska	Kamchatka
1	7/10	11	5	3	92
3	7/10	16	10	3	87
5	6/10	11	32	3	65
7	6/20	10	31	12	57
9	6/20	7	63	6	31

a cline of decreasing estimated proportion of Bristol Bay fish to the west. Asian fish are again indicated to occur in considerable proportion in sub-areas 7 and 9, and central Alaskan fish are shown to occur in low proportion.

Method of Estimating Catches of North American Sockeye

MOTHERSHIP FISHERY

There is little basis for deriving quantitative estimates of stock composition of sockeye catches by the mothership fishery other than the analysis by Fredin and Worlund (1974). Their method was used to update estimates of Bristol Bay sockeye interceptions by the fishery in 1971–77 (unpubl. U.S. National Marine Fisheries Service, NMFS, documents submitted to INPFC). Beginning with the 1978 catches, NMFS scientists have made the estimates by an abbreviated method based on averaged results of applying the original Fredin-and-Worlund method to data updated through 1976 (Table 2). The abbreviated method was required because beginning in 1978 virtually all of the statistical areas that had served to provide the Asian and Bristol Bay standard age compositions were excised from the fishery area.

Estimates of North American sockeye interceptions by the mothership fishery presented in this report are based on the following modifications of the NMFS estimates, which reflect my reconsideration of some of the original assumptions made by Fredin and Worlund (1974).

1. Bristol Bay maturing sockeye in sub-area 3. The assumption that all maturing sockeye in sub-area 3 are Kamchatkan is contradicted by recoveries in Bristol Bay of 10 fish tagged in this sub-area and by the occurrence of one *Triaenophorus*-infected fish (Fig. 7). Nine of the 10 tag recoveries were of age .3 fish, and all 10 recoveries plus three Kamchatkan recoveries of age .3 fish resulted from the release of 391 tagged maturing fish in the first 10-day period of June, 1961 (Aro et al. 1971; Kondo et al. 1965). Although Fredin and Worlund (1974) ultimately concluded that all fish in sub-area 3 are Asian, their initial analysis of migratory speed and timing indicated that maturing Bristol Bay fish might occupy at least part of sub-area 3 into early June, which is substantiated by all of the 11 Bristol Bay fish known from the sub-area. Interestingly, five of the 10 Bristol Bay tag recoveries were made on 10 or 11 July, just after the mid-date of the 1961 run, which suggests that Fredin and Worlund's (1974) assumptions about migratory speed are conservative.

The fraction of Bristol Bay fish in sub-area 3 catches through 10 June is unlikely to be as high as 77% (as suggested by the 1961 tagging results), even in years of peak Bristol Bay runs. Landrum and Dark (1968) applied discriminant analysis to morphological data taken from 1956–62 samples of maturing sockeye, and the average of the 20 estimates of contribution by the western Alaskan component (including stocks east to Kodiak) for sub-area 3 through 10 June was 20% (range 0% to 60%). I used Cook et al.'s (1981) classification results to calculate stock proportion estimates for sub-area 3 through 10 June and obtained 16 estimates (representing various age groups and years) that averaged 10% for Bristol Bay, 2% for central Alaska, and 88% for Asia. The 10% value is roughly one-third of the mean estimated contribution of Bristol Bay maturing fish in sub-area 5 through 10 June (Table 1B), so I assumed that the proportion of Bristol Bay fish in sub-area 3 in 1972–77 is one-third of that estimated by NMFS scientists for sub-area 5. The mean of the 1960–77 estimates for sub-area 5 from the Fredin-and-Worlund method is 46.3%, so I used

46.3%/3, or 15.4%, as an estimate of the proportion of Bristol Bay fish in the catches of maturing fish in sub-area 3 through 10 June in 1978–84.

2. Bristol Bay maturing fish in sub-area 5 in 11–20 June. Fredin and Worlund (1974) assumed that all fish in sub-area 5 in 11–20 June are maturing and of Asian origin. Because there is good evidence that Bristol Bay fish occur in sub-area 3 in early June, it is reasonable to assume that they would occur in the next sub-area east in the following 10-day period. Also, the mean of 1960–77 estimates for Bristol Bay made by Fredin and Worlund (1974) and subsequent authors for sub-area 5 in early June is 59.3%. These high estimates would suggest that some Bristol Bay fish occur in the same area in the following 10-day period. Unfortunately, Cook et al.'s (1981) classification results contained no records for this time/area stratum, so to determine a rough Bristol Bay stock proportion estimate I arbitrarily halved the NMFS estimates for the previous 10-day period for 1972–77, and used 59.3%/2, or 29.6%, for 1978–84.

3. Non-Bristol Bay maturing fish in sub-areas 7 and 9. Fredin and Worlund's assumption that all fish in these sub-areas through 20 June are of Bristol Bay origin is contradicted by results of tagging, morphological study, and scale analysis, which show occurrence of Asian and central Alaskan fish in these sub-areas. The mean estimated proportions of Asian fish in these sub-areas from scale analysis are quite high (57% and 31% in sub-areas 7 and 9, respectively; Table 1B). Landrum and Dark (1968) obtained 32 estimates of the proportion of Asian fish in these areas in May and June, which averaged 51% and 24% for sub-areas 7 and 9, respectively; these values are close to the mean proportions of 57% and 31% from scale analysis. I have assumed that through 20 June 40% and 20% of the maturing fish in sub-areas 7 and 9, respectively, are of Asian origin. The scale analysis provided low estimates of proportion of central Alaskan maturing fish in these sub-areas (Table 1B); for this paper I have assumed that 3% of the maturing fish in these sub-areas through 20 June are of central Alaskan origin.

4. Maturing fish in sub-areas 7 and 9 after 20 June, and in sub-areas 8 and 10 after 30 June. Fredin and Worlund (1974) assumed that any catches of maturing fish (ages .1, .3, and .4) in sub-areas 7–10 after the cut-off dates would be of miscellaneous western or central Alaskan origin. Since the great majority would be of western Alaskan origin, I added these late-season catches of maturing fish into estimates for the western Alaska category.

5. Bristol Bay immature fish in sub-area 3. All age .2 fish in sub-area 3 after 10 July were assumed by Fredin and Worlund (1974) to be immature and of Asian origin, but the recent scale analysis (Table 1A) indicated that even in June Bristol Bay immatures are found in the sub-area (unweighted mean of estimates is 18%). Also, Fredin and Worlund and other NMFS scientists obtained estimates of the proportion of Bristol Bay fish in the catches of age .2 immatures in sub-area 5 after 20 June that ranged from 1.0% to 94.9% and averaged 41.6%. It seems reasonable, then, that Bristol Bay fish would occur in sub-area 3, especially later in the season because of the strong westward migration of Bristol Bay immature sockeye south of the Aleutian Islands (French et al. 1976; Royce et al. 1968; French and Bakkala 1974). As a rough estimate, I assumed that the proportion of Bristol Bay fish in sub-area 3 after 10 July is one-third of the estimate for sub-area 5 after 20 June obtained by the Fredin-and-Worlund method for 1972–77, and 15% in 1980 and 1984 and 10% in other years after 1977 (the latter values are one-third of the appropriate values in Table 2).

6. Non-Bristol Bay immature age .2 fish in sub-areas 7 and 9. All age .2 fish in these sub-areas after 20 June were assumed by Fredin and Worlund to be immature and of Bristol Bay origin. However, tagging results show the presence of Asian immatures far east of 175°E in July (Fig. 8), and the estimated proportions of Bristol Bay immature fish recalculated from the recent scale analysis averaged 57% and 30% Asian fish in sub-areas 7 and 9, respectively, in June (Table 1A). Also, the mean estimated proportions from the scale study for central Alaskan fish were

TABLE 2. Abbreviated method, based on averaged results of Fredin and Worlund's (1974) original method, used by NMFS to provide estimates of catches of Bristol Bay sockeye by the mothership fishery after 1977. (Source: M. L. Dahlberg, NMFS, Auke Bay, Alaska, pers. comm.)

Part A: Average proportion of Bristol Bay fish by sub-area

Bristol Bay cycle year	Maturing		Immature age .2			
	Sub-area 5, through 10 June	Sub-area 6, through 20 June	Sub-area 5, after 20 June	Sub-area 6, after 30 June	Sub-area 8, after 30 June	Sub-area 10, after 30 June
Pre-peak	25	25	30	55	20	75
Peak	45	45	45	95	95	95
Post-peak	55	55	30	15	35	30
Mid-cycle	50	50	30	25	35	45

Part B: Average percentages of immature age .2 fish in mothership catches in times/areas of assumed intermingling of Asian and Bristol Bay immature sockeye.

Bristol Bay cycle year	Sub-area 5, after 20 June	Sub-area 6, after 30 June	Sub-area 8, after 30 June	Sub-area 10, after 30 June
Pre-peak	85	80	85	85
Peak	85	85	80	80
Post-peak	75	70	65	60
Mid-cycle	70	65	75	75

12% and 20%. Because of the early-summer westward migration of Bristol Bay immatures south of the Aleutians, the estimated proportions of Asian fish obtained in the scale analysis of June samples are undoubtedly too high to represent the situation after 20 June. Therefore, as a rough estimate I assumed that the proportion of Asian fish among age .2 immatures after 20 June is 10% in sub-area 7 and 5% in sub-area 9. Approximately 7% of the coastal tag recoveries from releases of immature sockeye in sub-area 9 in July have been from central Alaska. It is likely that central Alaskan fish are in less relative abundance in sub-area 7 than 9, so I have assumed that after 20 June, 5% of the immature age .2 fish in sub-area 7 and 10% of those in sub-area 9 are of central Alaskan origin.

The above six modifications represent simple additive adjustments to estimates calculated by the NMFS method, since they do not pertain to the areas/times of intermingling assumed by Fredin and Worlund.

Fredin and Worlund's (1974) method of estimating maturity composition also warrants examination. Beginning in 1977 Japan provided to the INPFC sockeye age and maturity composition data, stratified by 2°-latitude by 5°-longitude areas and 10-day periods, from research vessel and mothership operations. These 1977-84 data were coded and applied to similarly stratified mothership catch statistics. Direct estimates of age/maturity composition (i.e., age/maturity data for at least 25 fish sampled in the same 2° × 5° area and 10-day period as the catch) were used to prorate an average of 97% of the annual catches. When a catch occurred in a stratum for which there was no direct age/maturity estimate, age/maturity data from the entire sub-area/10-day period were used; these estimates were used to prorate an average of 2% of the catches. A third type of estimate, derived from "nearest" area(s) or "nearest" period(s), was used to prorate 1% of the catches, when sub-area/10-day period data were insufficient. The tabulation of the 1977-84 catches stratified by principal age/maturity group, sub-area, and 10-day period is too voluminous to present here, but the annual totals are shown in Table 3. The 1977-84 mean proportions of immature and maturing fish in each sub-area, stratified by Fredin and Worlund's (1974) assumption periods, are shown in Table 4.

Fish in the "other than age .2" category are essentially all age .3, as few age .1 fish are caught by commercial gillnet, and age .4 fish are in very low abundance. The age/maturity data indicate surprising numbers of immature age .3 fish given the low abundance of age .4 fish in high seas catches and in inshore runs. I suspect that the gonad weight criteria (Takagi 1961) used by Japanese scientists to determine maturity may be biased, at least for age .3 fish, indicating unrealistically high numbers of immature fish. Late-spawning fish may not begin gonad maturation as early as those that will spawn early, and some of these late-maturing fish may be considered immature on the basis of gonad weights measured in May and June. Osako (1973) mentioned that the proportion of fish maturing at age .4 is small, and that the error implied by assuming all age .3 fish as maturing would be small.

Table 4 shows that well over one-half of the fish of all age-groups caught before Fredin and Worlund's assumption dates are indeed maturing, but that there are also substantial proportions of immature fish. The proportions of maturing fish in the total catches are raised somewhat (by no more than 11% for any sub-area) if all non-age .2 fish are considered maturing, but there are still many immature age .2 fish in the early catches. The reverse is true in the later period, when Fredin and Worlund (1974) considered all age .2 fish to be immature; immature fish clearly make up the majority of the age .2 catches in an average year, but maturing fish made up averages of 16% to 46% of the catches in various sub-areas. There is considerable annual variability in maturity composition in both early- and late-season catches (see bracketed ranges, Table 4).

Despite the availability of these recent data on maturity composition, estimates of interception (i.e., high seas catch of North American sockeye) developed in this paper are based on Fredin and Worlund's original scheme, for the following reasons: (1) it reflects the overall shift from maturing to immature fish between early- and late-season catches; (2) annual variability of maturity composition is large, and even the average values in Table 4 are probably not good predictors of maturity composition in a particular sub-area and particular year in the 1972-76 period; and (3) there is insufficient information for determining stock composition for immature age .2 fish in early catches or for maturing age .2 fish in late catches.

As mentioned, interception estimates for the western Alaskan stock-group are derived by calculating estimates based on the Fredin and Worlund or NMFS method, and then adjusting them as outlined above. Estimates based on the Fredin and Worlund method for 1972-77 are taken directly from unpublished NMFS documents submitted to INPFC.

TABLE 3. Principal ocean age and maturity composition of sockeye catches by the Japanese mothership salmon fishery, in thousands of fish, 1977-84, based on age/maturity data provided by Japan.[a]

Year	All ages			Age .2		Other than age .2[b]	
	Total	Immature	Maturing	Immature	Maturing	Immature	Maturing
1977	1 389.0	437.7	951.3	391.5	490.6	46.2	460.7
1978	1 882.3	933.8	948.5	735.7	565.0	198.1	383.4
1979	2 185.6	1 213.2	972.5	1 103.1	434.4	110.1	538.1
1980	2 412.0	1 022.5	1 389.5	866.7	672.7	155.8	716.7
1981	2 223.7	1 392.7	831.0	1 252.6	485.7	140.2	345.2
1982	1 737.8	1 030.0	707.9	842.7	376.2	187.3	331.7
1983	1 655.1	1 032.6	622.6	924.3	299.5	108.3	323.1
1984	1 596.6	655.1	941.5	473.4	443.0	181.7	498.4

[a] See text for description of method of estimating age/maturity composition.

[b] Nearly all are age .3, as very few age .1 fish are caught by commercial gillnet and age .4 fish are in very low abundance.

TABLE 4. Mean proportions of immature and maturing sockeye (within age-group) caught by the Japanese mothership salmon fishery, in 1977–84[a]. Early (i.e., "Before") periods are when Fredin and Worlund (1974) assumed all fish in the sub-area are maturing, and late (i.e., "After") periods are when they assumed all age .2 fish are immature. Values in parentheses are the minimum and maximum annual percentages (sub-areas 1, 7 and 9 were fished only in 1977).

		Total catch		Age .2		Other than age .2	
Sub-area	Period	% immature	% maturing	% immature	% maturing	% immature	% maturing
1	Before 11 July	29 —	71 —	49 —	51 —	6 —	94 —
3	Before 11 July	31 (11–61)	69 (39–89)	40 (11–64)	60 (36–89)	20 (2–63)	80 (37–98)
5	Before 21 June	22 (7–38)	78 (62–93)	25 (10–44)	74 (56–90)	17 (6–28)	83 (72–94)
6	Before 1 July	39 (6–71)	61 (29–94)	48 (10–81)	52 (19–90)	26 (3–59)	74 (41–97)
7	Before 21 June	33 —	67 —	40 —	60 —	16 —	84 —
8	Before 1 July	38 (6–85)	62 (15–94)	47 (9–91)	53 (9–91)	20 (4–39)	80 (61–96)
9	Before 21 June	32 —	68 —	37 —	63 —	16 —	84 —
10	Before 1 July	20 (4–63)	80 (37–96)	25 (0–68)	75 (32–100)	17 (0–76)	89 (74–100)
3	After 10 July	76 (53–93)	24 (7–47)	83 (52–95)	17 (5–48)	43 (8–73)	57 (27–92)
5	After 20 June	66 (44–84)	34 (16–56)	74 (55–91)	26 (9–45)	35 (23–56)	65 (44–77)
6	After 30 June	77 (31–96)	23 (4–69)	80 (30–96)	20 (4–70)	56 (32–100)	44 (0–68)
7	After 20 June	53 —	47 —	67 —	33 —	22 —	78 —
8	After 30 June	63 (8–89)	37 (11–92)	71 (17–93)	29 (7–83)	32 (0–48)	68 (52–100)
9	After 20 June	48 —	52 —	54 —	46 —	11 —	89 —
10	After 30 June	61 (18–82)	39 (18–82)	67 (15–85)	33 (15–85)	35 (20–63)	65 (37–80)

[a] See text for description of how catches were prorated to age/maturity group. A catch of 119 281 sockeye in late May 1977 was excluded from calculation of the 1977 proportions as that was the only May catch in the entire 8-yr period.

My estimates for 1978–84 based on the "NMFS method," differ from those actually calculated by NMFS scientists, for the following reasons: (1) NMFS scientists have not used actual age composition data provided by Japan in recent years, but instead they estimated the numbers of age .2 fish in late-season catches by using average values shown in Table 2B. In contrast, my estimates of catch of age .2 fish are the result of prorating catches by actual age composition data; (2) NMFS scientists have developed estimates of interception of maturing Bristol Bay sockeye by considering only catches in sub-areas 5 and 6, whereas I have also included catches of all fish in sub-areas 8 and 10 through June 30, according to Fredin and Worlund's original method; and (3) NMFS scientists used "pre-peak" run values in Table 2 for 1984, whereas I used "pre-peak" values for 1983 and "peak" values for 1984.

LANDBASED DRIFTNET FISHERY

Estimates of interception of western and central Alaskan sockeye by the landbased driftnet fishery in 1972–81 were taken from Meyer and Harris (1983), who applied age/maturity data provided by Japan and stock composition estimates from Cook et al.'s (1981) and Knudsen and Harris's (1982) scale analyses to 1972–81 landbased sockeye catch statistics. They estimated stock composition only for catches of immature age 1.2 and 2.2 and maturing age 1.2, 2.2, 1.3, and 2.3 fish caught in May and June east of 160°E, which accounted for an average of 79% of the total annual catches. This same general approach was followed in updating the estimates to include 1982–84.

Meyer and Harris (1983) estimated contributions by two stock-groups, North American and western Alaskan, to the landbased driftnet catch. I assumed that the numbers of central Alaskan fish caught are the differences between Meyer and Harris's estimates for North American and western Alaskan stocks. These estimates for central Alaskan fish would also include small numbers of southeast Alaskan/B.C. maturing age 1.2 fish. Estimates for central Alaskan fish are made only for sub-areas 14 and 15, because Cook et al. (1981) suspected that some of the estimates for the far western areas were spurious.

Estimates of the age and maturity composition (with respect to the six principal age/maturity groups considered by Cook et al. 1981) of the May–June 1982–84 catches made east of 160°E were made in a manner similar to that described above for the mothership catches. Because there have been major gaps in research vessel sampling in the landbased area and because there is no biological sampling of landbased commercial catches, direct estimates (based on age/maturity data representing the same 2° × 5° area and 10-day period in which the catches occurred) were available for an average of only 13% of the annual catches. Age/maturity data stratified by sub-area/10-day period were used to develop estimates for 33% of the catches; and data from "nearest" areas or "nearest" periods were used to develop age/maturity composition estimates for an average of 54% of the catches. Because age/maturity data from the landbased fishery area were sparse, they were supplemented with data collected on motherships south of 48°N. Clearly, the estimates of age/maturity composition of the landbased catches are not as reliable as are those for the mothership catches.

Stock proportion estimates for the 1982–84 catches were derived from information in Meyer and Harris (1983). For each of the six principal age/maturity groups, the mean annual proportions of western and (for sub-areas 14 and 15) central Alaskan fish in each sub-area/month stratum were calculated. These mean stock proportions were then applied to the estimated catches stratified by age/maturity group, sub-area, and month.

Results and Discussion

AGE AND MATURITY COMPOSITION OF THE HIGH SEAS CATCHES

Table 5 provides total mothership catches of maturing and immature sockeye and estimates of catch of western and central Alaskan fish. There has been a shift from a predominance (mean 75%) of maturing fish in the catches in 1972–77 to a lower proportion (mean 46%) of maturing fish in 1978–84. Maturity compositions based on actual Japanese age/maturity data (Table 3) differ from those in Table 5 for individual years, but the average proportion of maturing fish in 1978–84 from Table 3 is 47% (55% if all non-age .2 fish are considered to be maturing), close to the average based on Fredin and Worlund's scheme. This recently lowered proportion of maturing fish in the annual catches is due mainly to the later timing of the mothership fishery (Fig. 5); most of the sockeye catch in 1972–76 was made in May and June, whereas in 1978–84 slightly over one-half of the total annual catch was made in July, when maturing fish are less abundant offshore.

Despite the recent shift to a higher proportion of immature fish in the mothership catches, the average weight of sockeye caught (obtained by dividing catches in weight by catches in numbers, from INPFC Statistical Yearbooks or Documents) has not decreased; the 1972–77 mean fish weight was 1.74 kg and the 1978–84 mean weight was 1.80 kg. This incongruity can be explained at least in part by the increase in average gillnet mesh size used by the fishery, beginning in 1978 as a result of USSR–Japan agreements. Before 1978 at least 40% of the nets set east of the Bulganin Line (at 170°25'E; see Fig. 3) had to contain 130 mm stretched measure mesh, whereas recently 130 mm web had to make up at least 60% of the nets set throughout the fishery area (Fredin et al. 1977 and Japan Fisheries Agency 1981). Gear selectivity for larger fish might be expected to cause a shift in age composition to older fish. Indeed, the mean proportion of non-age .2 fish (virtually all age .3) among the maturing component of the mothership catches increased from 48% in 1972–77 to 67% in 1978–84 (Table 6). The mean proportion of non-age .2 fish in total Bristol Bay runs has not increased in the post-1977 period (Table 6). Unfortunately,

TABLE 5. Total catches of maturing and immature sockeye by the mothership fishery, and estimates of interception of western (W.) and central (C.) Alaskan sockeye, in thousands of fish, 1972–84.[a]

	Maturing					Immature				
		Catch of W. Alaskan fish			Catch of C. Alaskan fish		Catch of W. Alaskan fish			Catch of C. Alaskan fish
Year	Total catch	From NMFS method	Adjustment	Total		Total catch	From NMFS method	Adjustment	Total	
1972	2 346.0	709.5	179.3	888.8	10.4	835.0	214.2	39.3	253.5	<0.05
1973	2 133.0	625.4	150.9	776.3	6.9	475.0	258.7	−4.9	253.8	6.4
1974	1 333.0	251.3	103.2	354.5	2.1	947.0	708.4	−72.8	635.6	36.6
1975	1 696.0	645.1	−103.4	541.7	13.3	471.0	221.7	−13.3	208.4	7.4
1976	1 793.7	778.7	−12.1	766.6	11.7	482.3	228.0	−8.9	219.1	13.7
1977	1 166.5	540.4	−1.8	538.6	7.7	341.2	327.8	−15.8	312.0	8.5
1978	861.7	126.2	105.7	231.9	0	1 020.5	294.4	3.9	298.3	0
1979	907.2	69.8	118.7	188.5	0	1 278.4	412.5	0.4	412.9	0
1980	1 130.3	178.9	118.6	297.5	0	1 281.7	578.9	8.1	587.0	0
1981	744.4	137.5	85.3	222.8	0	1 479.3	444.5	0.3	444.8	0
1982	772.9	65.7	154.2	219.9	0	964.9	302.8	0.6	303.4	0
1983	783.8	122.3	121.8	244.1	0	871.3	268.2	1.2	269.4	0
1984	998.2	123.7	177.4	301.1	0	598.4	320.3	10.1	330.4	0

[a] Total catches and estimates of interception of W. Alaskan fish ("from NMFS method") for 1972–77 are from U.S. National Marine Fisheries Service documents submitted to INPFC. Total catches in 1978–84 are the result of prorating stratified catches by recent age composition data (see text) but with respect to Fredin and Worlund's (1974) formula for estimating maturity composition. Estimates of interception for W. Alaskan fish ("from NMFS method") for 1978–84 are based on proportions in Table 2A (1980 and 1984 are considered Bristol Bay "peak" years), and, for maturing fish, all fish caught in sub-areas 8 and 10 in June. The "adjustment" column gives the net change to estimates from the NMFS method caused by consideration of broader intermingling than assumed by Fredin and Worlund (see text).

TABLE 6. Proportions of non-age .2 fish in mothership catches of maturing sockeye and in Bristol Bay inshore runs, and average weight of sockeye in mothership catches in all sub-areas after 10 July, 1972–84.

	Mothership catches of maturing fish[a]			Bristol Bay inshore runs[b]			
Year	Total catch	Catch of non-age .2	Percent non-age .2	Total run	Run of non-age .2	Percent non-age .2	Mean weight (kg) of fish in mothership catches after 10 July[c]
1972	2 346	937	40	5 373	2 666	50	1.44
1973	2 133	1 201	56	2 416	1 983	82	1.50
1974	1 333	849	64	10 932	2 109	19	1.50
1975	1 696	751	44	24 139	5 150	21	1.45
1976	1 794	626	35	11 493	4 285	37	1.58

TABLE 6. (*Continued.*)

Year	Mothership catches of maturing fish[a] Total catch	Catch of non-age .2	Percent non-age .2	Bristol Bay inshore runs[b] Total run	Run of non-age .2	Percent non-age .2	Mean weight (kg) of fish in mothership catches after 10 July[c]
1977	1 167	597	51	9 474	5 008	53	1.48
1978	862	582	67	19 653	8 343	42	1.59
1979	907	648	71	40 487	8 004	20	1.60
1980	1 130	873	77	62 276	16 039	26	1.66
1981	744	485	65	34 426	18 491	54	1.58
1982	773	519	67	22 222	17 121	77	1.71
1983	784	431	55	45 416	8 530	19	1.54
1984	998	680	68	40 719	12 307	30	1.74
Mean, 1972–77			48			44	1.49
Mean, 1978–84			67			38	1.63

[a] Catches, in thousands of fish, are from U.S. National Marine Fisheries Service Documents submitted to INPFC for 1972–77, and from Tables 3 and 6 for 1978–84.

[b] Runs, in thousands of fish, are from Bristol Bay sockeye age composition tables provided by the Alaska Department of Fish and Game.

[c] Calculated from INPFC Statistical Yearbooks for 1972-81, and from INPFC Documents for 1982–84.

information on age composition of total Asian runs for the 1972–84 period is not available. The average weight of fish in mothership catches after 10 July in all sub-areas increased from 1.49 kg in 1972–77 to 1.63 kg in 1978–84, indicating that the size of (mostly) immature fish also increased in the recent period (Table 6). The increase in size of immatures might have also been caused in part by improvements in growth conditions in the northeastern Pacific from the early 1970's to the late 1970's and early 1980's (Rogers 1984). However, the shift in age composition of captured maturing fish in addition strongly suggests a response to the increase in gear mesh size.

Cook et al.'s (1981) data permitted estimation of age/maturity composition only for landbased driftnet catches of sockeye made in May and June east of 160°E, which accounted for an average of 95% of the 1972–84 total catches (Table 7). Catches in July averaged about 4% of the total annual landbased driftnet sockeye catches. Because of the averaging and pooling of Japanese age/maturity data done by Meyer and Harris (1983) and in the present study to cover major gaps in research vessel sampling in the landbased fishery area, the age/maturity composition estimates presented in this paper are probably very rough. For instance, much of the age/maturity data used came from mothership samples collected between 46°N and 48°N, and these data likely show higher proportions of maturing and older fish than actually occurred in landbased fishery catches.

Catches of immature age 1.2 and 2.2 and maturing age 1.2, 2.2, 1.3, and 2.3 sockeye in May and June east of 160°E averaged 80% of the total 1972–84 landbased catches (Table 7). Meyer and Harris (1983) noted that the majority of the fish in the other age/maturity groups consisted of freshwater

TABLE 7. Estimated age/maturity composition of May-June sockeye catches east of 160°E by the Japanese landbased driftnet fishery, 1972–84.[a]

Year	Total catch	May–June catch west of 160°E	Catch in July	May–June catch east of 160°E Total	Immature Age 1.2 & 2.2	Maturing Age 1.2 & 2.2	Maturing Age 1.3 & 2.3	Other age/maturity groups
1972	3 710.7	41.9	340.8	3 328.0	1 624.2	890.8	97.4	715.6
1973	3 308.1	25.0	86.7	3 196.4	993.9	1 315.8	224.3	662.4
1974	3 155.0[b]	38.0	111.0	3 002.0	1 165.5	972.5	234.4	629.6
1975	2 968.0	19.0	79.0	2 870.0	734.5	1 649.2	154.6	331.7
1976	3 504.2	74.0	300.5	3 129.7	908.6	1 597.2	175.1	448.7
1977	1 289.3	3.4	52.2	1 233.8	638.9	284.1	56.5	254.2
1978	1 292.6	12.5	12.7	1 267.5	705.0	168.0	139.7	254.7
1979	756.6	2.6	9.8	744.2	261.4	351.3	49.4	82.1
1980	787.0	6.5[c]	76.8	703.8	382.3	120.3	104.7	96.5
1981	858.0	10.7	28.9	819.1	333.8	235.5	149.2	100.6
1982	723.2	18.7	4.1	700.4	130.2	406.9	119.6	43.8
1983	828.3	15.1	7.9	805.2	252.3	171.8	251.6	129.6
1984	305.3	11.3	0.4	293.6	115.6	92.5	36.5	48.9

[a] Catches are in thousands of fish. Original source of statistics is INPFC Documents. 1972–81 values are from Meyer and Harris (1983); see text for description of how 1982–84 values were calculated.

[b] Catches by 2° × 5° areas in original document do not add up to total reported for 1974.

[c] A small catch in area E6550 was added to this column by Meyer and Harris (1983), but it was prorated to age/maturity group in the present table.

age 3. fish (of all ocean ages and maturity groups) and immature ocean age .3 fish. Again, it is possible that some of the age .3 fish assessed as immature were actually maturing. The mean proportion of immature fish within the six principal age/maturity groups was 46% in both 1972–77 and 1978–84 periods. The lack of a shift in maturity composition is not surprising, as there was no marked shift in the timing of the landbased fishery, as occurred in the mothership fishery (Fig. 6). Within the maturing component, there was a shift toward higher proportion of age .3 fish in the recent period. This echoes the finding for the mothership fishery, but it likely resulted from use of age/maturity data for the southern mothership area to prorate a large fraction of the landbased catches.

CATCHES OF NORTH AMERICAN SOCKEYE

Table 5 presents estimates of the numbers of immature and maturing western and central Alaskan sockeye caught by the mothership fishery. For western Alaskan fish, the table shows the estimates as calculated by the Fredin-and-Worlund or NMFS method (the latter is based on average stock composition values in Table 2A), and adjustments based on my assumptions of wider intermingling of Asian and western Alaskan stocks. For most years, the adjustments resulted in increased estimates of catch, and in later years the adjustments for maturing fish were sometimes greater than estimates based on the NMFS method. For some years in the mid-1970's, however, the adjustments were negative because of spatial distribution of the catches relative to the revised assumptions regarding stock proportions.

The estimated catches of central Alaskan fish are based on static, low stock composition estimates for sub-areas 7 and 9, and while their accuracy is questionable they at least account for some low catch of this stock-group in these subareas before 1978, and show that the numbers of central Alaskan fish caught were far less than those of western Alaskan fish. No quantitative estimates were made for the southeast Alaska/British Columbia stock-group, but a few fish (mostly immatures) from this region would have been caught by the pre-1978 mothership fishery and virtually none are caught now.

Table 8 shows the estimated catches of western and central Alaskan fish and proportion of these in total mothership fishery catches of maturing and immature sockeye. The catches of maturing sockeye in the 1978–84 period averaged about 885 000 fish, about one-half of the 1972–76 mean catch of 1 860 000 fish. This decrease is largely due to the prohibition of May fishing imposed by the new Annex to the North Pacific Treaty Protocol, but also to the overall reduction in size of the fishery and the new, more restrictive quotas. The estimated catch of maturing Alaskan sockeye decreased even more sharply than the total catches, averaging about 244 000 fish in 1978–84 or about a 64% reduction from the 1972–76 mean of 674 000 fish. This marked reduction of catch of maturing Alaskan sockeye is due to the prohibition of fishing in the sector southeast of 56°N, 175°E, where Alaskan fish greatly predominate. The proportion of Alaskan fish in the catches of maturing fish also decreased, but only modestly from 36% to 28%. This is due to the exclusion of sub-area 1 and all but a small section of sub-area 3, that had the effect of pushing the fishery eastward (mostly east of 170°E) where significant intermingling of Alaskan and Asian sockeye occurs. Thus, there were two major area restrictions that had opposing effects; the exclusion of the area southeast of 56°N, 175°E tended to decrease the proportion of Alaskan fish in the catch whereas the exclusion of sub-areas 1 and most of 3 tended to increase it.

The picture for immature sockeye is somewhat different, but still involves the offsetting effects of fishing area restric-

TABLE 8. Total catches (in thousands of fish) of maturing and immature sockeye by the Japanese mothership fishery and estimated number and proportion of western and central Alaskan sockeye caught, 1972–84.

	Maturing			Immature		
		Catch of Alaskan fish			Catch of Alaska fish	
Year	Total catch	No.	%	Total catch	No.	%
1972	2 346.0	899.2	38	835.0	253.5	30
1973	2 133.0	783.2	37	475.0	260.2	55
1974	1 333.0	356.6	27	947.0	672.2	71
1975	1 696.0	555.0	33	471.0	215.8	46
1976	1 793.7	778.3	43	482.3	232.8	48
1977	1 166.5	546.3	47	341.2	320.5	94
1978	861.7	231.9	27	1 020.5	298.3	29
1979	907.2	188.5	21	1 278.4	412.9	32
1980	1 130.3	297.5	26	1 281.7	587.0	46
1981	744.4	222.8	30	1 479.3	444.8	30
1982	772.9	219.9	28	964.9	303.4	31
1983	783.8	244.1	31	871.3	269.4	31
1984	998.2	301.1	30	598.4	330.4	55
Mean, 1972–76	1 860.3	674.5	36	642.1	326.9	50
Mean, 1978–84	885.5	243.7	28	1 070.6	378.0	36
% change	−52%	−64%	−22%	+67%	+16%	−28%

tions imposed by the 1978 North Pacific Treaty Annex and by the new USSR–Japan agreement. The mean total annual mothership catches of immature fish increased greatly, from about 642 000 fish in 1972–76 to 1 071 000 fish in 1978–84. This is largely attributed to the recent heavy concentration of late-season fishing in sub-area 5, where sockeye abundance is high (Fig. 5). In 1978–84 an average of 1.35 million tans (about 60 750 km) of gillnet was fished in sub-area 5 after 20 June each year as compared to an average of 0.34 million tans (about 15 300 km) in 1972–77. The recent catch of Alaskan immature sockeye has also increased, but only by 16% over the 1972–76 mean catch. Under the recent regulatory regime an average of about 379 000 immature western Alaskan sockeye has been caught annually by the mothership fishery. The proportion of Alaskan sockeye in the catches of immatures, however, decreased after 1977, from about 50% to 36%. This reduction is due to exclusion of the sector southeast of 56°N, 175°E, and as in the case for maturing sockeye, this decrease was not great because of the offsetting effects of excluding sub-areas 1 and most of 3.

The effects of excluding sub-areas 1, 7, 9, and most of 3, 8, and 10 from the mothership fishery can be better understood by examining the change in average longitude of sockeye catch. The statistics are coded by 5°-longitude interval for 1972–77 and by 1°-interval after 1977, but for consistency I calculated average longitude of total annual sockeye catches based on 5°-interval codes. In 1972–76 the mean longitude of total sockeye catch was 169.2°E, and the range was 168.2°E to 170.3°E. In 1978–84, the mean was 170.4°E and the range was 169.9°E to 171.0°E. Thus, despite the closure of significant areas east of 175°E, the net effect of the combined area changes imposed by the revised treaties was to shift the sockeye fishery slightly eastward, closer to Alaska. Interestingly, Table 8 shows that Alaskan sockeye comprised the highest fraction of the mothership catches of both maturing and immature sockeye in 1977. In that year (when the USSR 200-mi zone was closed but the area southeast of 56°N, 175°E was still open), the mean longitude of sockeye catch was farther east (171.8°E) than in any other year in the 1972–84 period.

Estimates of catch of western and central Alaskan sockeye by the landbased fishery were made for the six principal age/maturity groups, in May and June east of 160°E. Although stock composition was not estimated for catches in minor age/maturity groups or for July catches, some inferences regarding continental origins of these catches is possible. Harris and Meyer (1982) concluded that most of the fish in the minor age/maturity groups (mostly freshwater age 3. and immature ocean age .3) would be of Asian origin, due to the much higher proportions of freshwater age 3. fish and ocean age .4 fish in Kamchatkan runs than in western Alaskan runs. Fish caught in July would be virtually all immature, and might have a continental stock composition generally similar to that of immatures in June.

The estimated catches of western and central Alaskan sockeye by the landbased driftnet fishery are shown in Table 9, along with the total catches for which estimates could be made. As was the case for the mothership fishery, the great majority of the Alaskan fish caught was of western Alaskan origin. The low estimated catches of central Alaskan fish are due largely to my assumption that central Alaskan fish oc-

TABLE 9. Total May–June catches of immature age 1.2 and 2.2 and of maturing age 1.2, 2.2, 1.3, and 2.3 sockeye by the landbased driftnet fishery east of 160°E, and estimates of interception of western and central Alaskan sockeye, in thousands of fish, 1972–84.[a]

	Maturing					Immature				
		Estimated catch of Alaskan fish					Estimated catch of Alaskan fish			
Year	Total catch	Western Alaskan	Central Alaskan	Total	Percent Alaskan fish in catch	Total catch	Western Alaskan	Central Alaskan	Total	Percent Alaskan fish in catch
1972	988.2	92.2	3.0	95.2	10	1 624.2	168.2	27.3	195.5	12
1973	1 540.1	73.2	7.9	81.1	5	993.9	104.5	23.6	128.1	13
1974	1 206.9	73.3	3.4	76.7	6	1 165.5	132.5	20.0	152.5	13
1975	1 803.8	57.3	0.7	58.0	3	734.5	64.9	6.6	71.5	10
1976	1 772.3	287.9	29.7	317.6	18	908.6	69.0	6.8	75.8	8
1977	340.6	36.4	<0.05	36.4	11	638.9	47.0	<0.05	47.0	7
1978	307.7	28.9	0	28.9	9	705.0	56.5	0	56.5	8
1979	400.7	26.8	0	26.8	7	261.4	22.8	0	22.8	9
1980	225.0	21.2[b]	0	21.9	9	382.3	37.4	0	37.4	10
1981	384.7	36.2	0	36.2	9	333.8	33.4	0	33.4	10
1982	526.5	54.7	<0.05	54.7	10	130.2	15.4	<0.05	15.4	12
1983	423.4	56.0	0	56.0	13	252.3	20.1	0	20.1	8
1984	129.0	12.8	0	12.8	10	115.6	7.8	0	7.8	7
Mean, 1972–76	1 462.3	116.8	8.9	125.7	8	1 085.3	107.8	16.9	124.7	11
Mean, 1978–84	342.4	33.8	<0.05	33.8	10	311.5	27.6	<0.05	27.6	9
Percent change	−77%			−73%	+25%	−71%			−78%	−18%

[a] 1972–81 values are from Meyer and Harris (1983); see text for description of how estimates were derived for 1982–84.

[b] A small catch in area E6550 in 1980 was ignored by Meyer and Harris (1983), but was prorated to age/maturity group and to stock-group in the present table.

cur only east of 175°E; the estimates would have been considerably higher (but still much lower than those for western Alaskan fish) if Cook et al.'s (1981) stock proportion estimates for central Alaskan fish west of 175°E had been applied. The estimates for central Alaskan fish include small numbers of southeast Alaskan/B.C. maturing are 1.2 fish. Small numbers of maturing and immature fish from this region were likely caught in sub-areas 14 and 15 before 1978, but virtually none have been caught by the landbased fishery west of 175°E.

The landbased catches of maturing and immature sockeye greatly decreased in the recent period, to just over 650 000 fish, or about one-quarter of the 1972–76 catch levels. This decrease has been largely due to the exclusion from the fishery of most of the area north of 44°N, and to the general decrease in size of the fleet necessitated by reduced quotas. The effect on sockeye catches of removing areas north of 44°N from the fishery can be illustrated by analysis of CPUE and catch distribution. The 1972–77 mean May-June CPUE of sockeye by the landbased fishery between 160°E and 175°E and between 44°N and 46°N was 1.01 fish/tan of gillnet, whereas the CPUE between 42°N and 44°N was only 0.20 fish/tan. The prior importance of the area north of 44°N is further attested by the fact that an average of 99% of the 1972–76 annual landbased sockeye catch was made north of this latitude. The removal of the area east of 175°E from the landbased fishery area had little direct effect on sockeye catches, as fishing in that sector contributed only about 9% of the total annual sockeye catch before 1978 (Fig. 6; Meyer and Harris 1983).

The mean catch of Alaskan sockeye by the landbased fishery has decreased greatly as well, from about 126 000 fish to 34 000 fish for the maturing component, and from 125 000 fish to 28 000 fish for immatures. The proportion of Alaskan fish in the landbased fishery catches essentially did not change after 1977; the slight changes indicated in Table 9 are not considered significant given the low level of precision of the compounded estimates of age/maturity and stock composition. Meyer and Harris (1983) noted that the proportion of western Alaskan sockeye in landbased catches east of 175°E was considerably higher than west of 175°E. However, the exclusion of the area east of 175°E did not significantly reduce the proportion of Alaskan fish in the total catch, as only a small fraction of the total catch had previously been made in that area.

ASSUMPTIONS

Clearly, the estimates made in this paper and by Fredin and Worlund (1974) and Meyer and Harris (1983) are based on numerous assumptions, and must be qualified accordingly. One major assumption pertains to the accuracy of the commercial mothership and landbased catch statistics. There is considerable in-season monitoring of the mothership fishery by the Japan Fisheries Agency and, in recent years, by USSR and U.S. observers, which might give some credence to the statistics. However, there is poor surveillance of the landbased fishery, statistics for the fishery are compiled from fishermen's reports, and landbased driftnet salmon vessels have been observed far north and east of their authorized fishing area (Fredin et al. 1977). Even recent landbased statistics have shown fishing activity as far north as INPFC statistical area E6550, which is over 360 n.mi. north of 44°N between 165°E and 170°E. The spatial/temporal distribution as well as the overall magnitude of the landbased catches are therefore in question.

One of the major assumptions made by Fredin and Worlund (1974) is that respective age compositions of Asian and Bristol Bay sockeye in areas of assumed intermingling are the same as in areas of assumed pure populations. This assumption is questionable, as scant evidence suggests that age .3 Bristol Bay fish might be distributed farther west than age .2 fish, and Rogers (Fisheries Research Institute, Univ. Washington, Seattle, pers. comm.) analyzed tag recovery data suggesting that stocks from the various Bristol Bay river systems, which have differing age compositions, might have different patterns of ocean migration although the limits of their distributions may be similar.

Fredin and Worlund's (1974) assumption regarding maturity composition of age .2 fish was found to be reasonably accurate, although there were major deviations for individual sub-areas and years. Such variations of maturity composition would suggest error in the stock composition estimates based on age composition. I attempted to adjust estimates of mothership catches of Alaskan fish based on Fredin and Worlund's (1974) method by accounting for presence for non-Bristol Bay fish east of 175°E and for presence of Bristol Bay fish in additional 10-day/sub-area strata west of 175°E. Any broadening of the area of assumed intermingling implies error in Fredin and Worlund's (1974) and subsequent original estimates, as Bristol Bay and Asian "standard" age compositions are now thought to be based in part on mixed-stock samples. However, the newly assumed proportions of Bristol Bay fish west of 170°E and of non-Bristol Bay fish east of 175°E are low relative to the total samples forming Fredin and Worlund's standard age compositions.

Meyer and Harris (1983) outlined several assumptions required in their estimation of landbased catches of North American sockeye, which included all those in the original scale pattern study by Cook et al. (1981). Of particular concern is the averaging and pooling of both age/maturity data and stock proportion estimates required to cover major gaps in biological sampling of sockeye south of 46°N.

A major assumption pertaining to estimates of both mothership and landbased catches of Alaskan sockeye in recent years is that stock composition in areas of high seas intermingling was roughly the same after 1977 as before. The 1978–84 mothership estimates were based in part on averaged values in Table 2A. Similarly, the 1977–84 landbased estimates were based on averaged results of Cook et al.'s (1981) analysis of 1972–76 scale data. The relative abundance of western Alaskan sockeye greatly increased beginning in 1978 (Table 10), due mostly to natural factors affecting production although the reduction of the high seas fisheries was undoubtedly a contributing factor (Rogers 1984). Estimated sockeye runs to the USSR in 1978–83 have averaged about 2.6 times the 1972–77 mean run, but the recent western Alaskan runs have averaged about 3.7 times the 1972–77 mean run. The markedly higher recent CPUE of sockeye in sub-areas 3 and 5 in June and July (Fig. 5) may be in part due to increased abundance of Asian and Alaskan runs. The greater relative increase of western Alaskan sockeye runs

TABLE 10. Abundance of Asian and North American sockeye salmon stocks in 1972-84, in millions of fish.[a]

Year	USSR[b]	Western Alaska	Central Alaska	S.E. Alaska to Washington
1972	0.7	6.2	5.4	8.4
1973	1.3	3.0	4.7	14.9
1974	0.9	11.5	5.3	13.5
1975	1.1	24.9	3.9	6.9
1976	0.8	13.0	7.9	9.5
1977	1.3	10.7	10.1	13.3
1978	2.5	21.9	9.1	13.2
1979	2.3	44.0	7.0	12.2
1980	2.7	68.2	8.0	7.1
1981	2.7	39.5	10.1	14.9
1982	2.1	26.6	12.7	20.1
1983	3.0	51.4	13.6	10[c]
1984	—	45.9	12.6	8[c]

[a] All North American run estimates are from D. Rogers (Fisheries Research Institute, Univ. Washington, Seattle, pers. comm.).

[b] Run estimates for USSR stocks are twice the catch, under the assumption that inshore exploitation rate is 50%. 1972–75 catches in numbers are from INPFC (1979), 1976–77 catches in weight are from unpublished tables provided by INPFC, 1978–79 catches in numbers provided by TINRO, 1980–83 catches in weight are from FAO Yearbook of Fishery Statistics, Vol. 56. Catches in weight were converted to numbers by applying average weight of 2.834 kg/fish, calculated from 1962 to 1975 data (INPFC 1979).

[c] Rough estimate based on preliminary or incomplete catch data.

begs the question of whether the western Alaskan stock proportions in areas of high seas intermingling have been higher since 1977 than before.

Stock composition of sockeye on the high seas would be influenced not only by relative abundance of regional stocks, but also by variations in their distributions caused by oceanographic conditions. Burgner (1980) showed that the timing of inshore runs of Bristol Bay sockeye is influenced by temperature conditions during the spawning migration. Scientists of the International Pacific Salmon Fisheries Commission (IPSFC) have shown that the migratory timing and routes of maturing Fraser River sockeye are affected by sea surface temperatures (IPSFC 1985). However, there is not enough information on effects of oceanographic conditions on migratory timing and routes of immature and maturing Asian and Alaskan sockeye to account quantitatively for such effects in the present analysis.

Conclusions

Provisions of the revised (1978) North Pacific Treaty Annex certainly had the desired effect of protecting Alaskan sockeye from catch by the Japanese high seas salmon fisheries. For the mothership fishery, the prohibition of all fishing in May and of fishing in the U.S. 200-mi zone before 10 June has helped to reduce the catch of maturing fish. The closure of the sector southeast of 56°N, 175°E served to protect many western Alaskan maturing sockeye migrating east out of the central Aleutian area in May and June. The same area closure also reduced potential catches of Alaskan immature fish. Although total mothership catches of immature sockeye have greatly increased in recent years, the catches of western Alaskan fish have only modestly increased because of prohibition of fishing southeast of 56°N, 175°E. Clearly, the area closures imposed through the USSR–Japan agreements would have caused greatly increased catches of Alaskan fish had the restrictions in the 1978 North Pacific Treaty Annex not been imposed at the same time. The eastward shift of mothership fishing effort in 1977 and the concomitantly increased proportion of Alaskan sockeye in the 1977 catch suggest what might have occurred without the revised Annex. However, the 1978 North Pacific Treaty Annex has probably had relatively little effect in saving western Alaskan fish from capture by the landbased fishery, although it has precluded any major eastward shift of landbased fishing effort that might have occurred in the face of USSR–Japan restrictions.

High seas exploitation of Alaskan sockeye has been reduced by provisions in the 1978 North Pacific Treaty Annex, but also by provisions of the recent USSR–Japan agreements. These agreements included elimination of most of the previous landbased fishery area north of 44°N where virtually all of the landbased sockeye catch had been made. As mentioned, closure of the area east of 175°E had little effect on stock composition of the landbased sockeye catch, and the great decrease in catch of Alaskan sockeye by this fishery is due almost entirely to closure of the area northwest of 44°N, 170°E and to the overall reduction of fishing effort and catch. The recent USSR–Japan agreements have included a new, restrictive quota system that forced reduction of both fisheries, from 332 mothership catcherboats in 1972–76 to 172 in 1978–84 and from over 300 landbased vessels in the mid-1970's to 209 in 1978–84. The concomitant decreases in fishing effort and total sockeye catch (Fig. 1 and 2) certainly helped reduce catches of Alaskan as well as Asian sockeye. Had the restrictions imposed through USSR–Japan agreeement not been in effect, the catches of Alaskan fish by both fisheries would probably have been much higher, even in the face of the restrictions in the revised 1978 North Pacific Treaty Annex.

The recent savings of Alaskan fish from high seas capture are therefore due to the combined effects of the revised North Pacific and USSR–Japan treaties, and not to the North Pacific Treaty Annex alone. Vronskii and Senilnikov (1985) stated that through the tripartite treaty the United States and Canada practically excluded the influence of the Japanese fishery on salmon stocks of Canadian and North American origin, but I believe this is an overstatement. Significant catches of Alaskan sockeye continue to be made by the mothership fishery and, without the catch limits imposed by the USSR-Japan agreements, there is still potential for much larger catches of Alaskan sockeye.

It would be extremely difficult, and in some cases virtually impossible, to test the numerous assumptions in this analysis. Some assumptions might be examined through computer simulation studies, and Fredin and Worlund's age composition method could be reapplied to all 1960-77 data to determine whether my revised assumptions regarding areas of intermingling would affect greatly the estimates of catch of western Alaskan sockeye in sub-areas 5, 6, 8, and 10. Also, scale patterns in recent samples could be analyzed to determine whether stock proportions, particularly in the mothership area, have changed markedly with the great increase in relative abundance of Alaskan sockeye. Such continued studies would provide the means for improving the accuracy of the stock composition estimates presented herein. However, I doubt that they would change my overall conclusions that high catches of Alaskan sockeye have been lower in 1978-84 than in 1972-76, that the proportion of Alaskan fish in the high seas catches of sockeye has changed relatively little, and that the recent savings in Alaskan fish are due to the combined effects of the new North Pacific Treaty Annex and of the USSR-Japan agreements.

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Special Guest Lecture

From Rubber Boots to Recombinant DNA: Sockeye Research in the Past 35 Years

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The other day I was reading again one of my favorite books, "A Stress Analysis of a Strapless Evening Gown." One of its many "one-liners" needs only a slight modification to describe my dilemma in addressing you this evening: an after dinner speech is a social event designed to bring the minimum pleasure to the maximum number of people. A published paper stands at the other end of the spectrum since it gives maximum pleasure to the minimum number of people (Weaver 1963). Because this address is supposed to be published, you can see my problem.

I decided, therefore, to follow the well-tried recipe of devoting two-thirds of my time to history, which many of us would just as soon forget, and one-third to the future, which none of us can foresee, hoping that this mixture will strike some responsive chords and create some harmless amusement. At the same time I intend to quote some statistics to give the editors an impression of science. I have also written a technical appendix which should ensure publication even though no one will read it except the editor and me.

Back in the olden days when I was a graduate student, it was typical of ecologists that they made a career of studying one kind of animal. There was the fellow who studied pheasants, the other fellow who studied rabbits, another moose, and another trout or whitefish or ciscoes.

One of the jokes of those days was that if you worked on any one species long enough, you began to look like it and to act like it. I remember a young lady who was quick, nervous, twitchy, wore tweeds and had agouti colored hair: she studied mice. So, those of you who are green about the gills, otherwise flushed and look like sockeye now know why.

In those days, when it came to salmon, there was sharp specialization: one species-one ecologist was the idea. There was the pink salmon guy, the chinook guy, and so on. The oldest local sockeye specialist was W. A. Clemens (1935, 1938) who for many years read scales and, building on the early work of Gilbert (1913, 1914–25), compiled statistics of the catch and encouraged young people to do research on the many questions that were posed by the biology of the sockeye. Among his many other achievements, Clemens hired Ricker and Foerster and started them on studies of juvenile sockeye in Cultus Lake.

At that time there had been amassed by various workers in British Columbia and the United States, especially Alaska and Kamchatka, considerable knowledge of the natural history of sockeye salmon. It was strongly held, mostly on the basis of circumstantial evidence, that sockeye returned to their home streams. I recall that A. G. Huntsman, a noted critic and skeptic who worked on Atlantic salmon, pointed out that salmon did not return to their home streams *to* spawn. They returned to their home streams *and* spawned. He also wasn't too sure that they did home; and if they did, he wasn't certain they ever "went out of the influence of their stream of origin." If they did go beyond the influence of their home streams, he wasn't certain whether those who found home didn't just blunder into it by random movement; and he wasn't certain he knew what random movement was either. A great scientist!

The places where sockeye spawned were well catalogued and various witchcrafts of artificial propagation, including perjury, were well developed. The variable period of freshwater residence, usually in lakes, was well documented. Fragments of information were available from tagging studies and high seas catches about the marine migrations of sockeye. The mysteries of cyclic dominance were beginning to generate theories of population dynamics. To read about it all up to the 1960's, one has only to go to Earl Foerster's bulletin on the sockeye (Foerster 1968).

The tools of the trade for sockeye biologists in those days were a pair of rubber boots, a microscope, a field notebook and, as George Spencer, the entomologist, used to add, a pencil and a life insurance policy. The professional skills included how to fix an outboard motor and how to cook a meal on a Coleman stove. Despite these primitive tools, by 1950 the stage was well set for all that followed. It is hard to find any phase of sockeye biology that hadn't been opened up prior to World War II.

The fisheries of those days were everywhere regulated by a seat-of-the-pants technique which featured a fair amount of cops and robbers kind of action. It was widely recognized that rates of exploitation were on the high side and that the future depended on tighter regulation of catches. The IPSFC (International Pacific Salmon Fisheries Commission) was a burgeoning young organization with a territorial imperative for managing Fraser River sockeye even though the terms of reference weren't written quite that way. There were rumblings about the need to set up a special management committee for the Skeena River fishery, a clamor to more closely regulate the Alaska fisheries, and the dawning of the realization that the high seas fisheries on the other side of the Pacific might be taking fish of North American origin.

In these circumstances — lots of unanswered biological questions and the need for better regulation of the fisheries — there was a period of rapid growth in all of the salmon research and management agencies in North America. In less than a decade virtually all aspects of sockeye salmon biology were attacked on a broad front. The Pacific Fishery Biologists, a highly informal annual assembly (most of them salmon biologists who didn't believe in wearing ties — they cut off your tie at the stumps) was the major vehicle for exchanging information and political excuses. (That same organization is now four times as large and has female members, so in some ways at least, it is considerably better behaved than it used to be.)

This is not the time or place to review the many individual contributions to sockeye biology, nor to detail the major findings of the past 40 years of sockeye research but a few statistics may paint the picture. I've chosen to deal only with the publications of the Fisheries Research Board as a more or less representative sample (and much the easiest to compile) from the indices of Neal Carter (1968, 1973) and thereafter the annual Fisheries Research Board indices (1973–79).

The publications on salmon were tallied by my assistant, Moira Greaven, with respect to ten categories: life history and growth, ecology and pollution, behavior and migration, parasites and diseases, population dynamics and management, physiology, enhancement, anatomy and systematics, ageing techniques, and methodologies of other kinds. The tallies were kept for each of the five species and for Pacific salmon as a group and then lumped for presentation as concerning sockeye and kokanee, pink and chum, coho and chinook, and all species as a group.

The results of this analysis were a tedious demonstration of the obvious which I will nevertheless tell you about. If some of the dates seem a bit odd to you, bear in mind that I analyzed the publications, not the research that was done, and as you all know, the time lag between doing the research and getting it published varies from a few months to infinity with a mean of a few years.

In the 1950's (Table 1) the publications of the Fisheries Research Board of Canada relating to Pacific salmon in general and sockeye in particular were dominated by contributions to life history and growth, migrations (chiefly tagging studies), and population dynamics and management. The counting of sockeye going upstream and downstream was a virtual mania. Tagging studies and further filling in of the details of life history were the other principal addictions, particularly as the data for the International North Pacific Fisheries Commission studies began to appear. In brief, the 1950's were a logical continuation of what had gone before, with more people doing it, and strong emphasis (almost a third of the total publications) on that most famous of all Pacific salmon, the sockeye.

In the 1960's (Table 2), when many of the army of new researchers were beginning to publish in earnest, the total number of publications on Pacific salmon of all species increased from 279 in the 1950's to 481 in the 1960's, an increase of 72%. Physiology dominated, partly because it was seen to be fundamental to understanding such questions as "Why do salmon go to sea when they do?", which was a good basic biological question, and "What are their capabilities for swimming performance?", which was not only a good basic biological question, but highly relevant to the impact of hydroelectric dams. (It was the dream of every young civil engineer of those days to design either a highway or a dam.) In addition there was a sustained interest in population dynamics and management, and large increases in the number of publications on parasites and diseases, anatomy and systematics, ageing techniques, and a wide range of methodologies particularly concerned with estimating numbers of sockeye, most of which were not very reliable and none of which seemed to be all that useful after the data had been collected.

Of all of the species of salmon the sockeye was the most published about, still accounting for roughly a third of the total. The 1960's were evidently a period of intense research activity with a strong emphasis on relatively basic science

TABLE 1. Publications of the Fisheries Research Board of Canada in the 1950's that concerned Pacific salmon.

	Sockeye and Kokanee	Pink and Chum	Coho and Chinook	Pacific Salmon as a Group	Total	%
Life History Growth	18	13	21	11	63	23
Ecology Pollution	11	3	2	4	20	7
Behavior Migration	16	28	29	3	76	27
Parasites Diseases	4	2	1	1	8	3
Population Dynamics Management	20	22	14	5	61	22
Physiology	15	6	6	1	28	10
Enhancement	0	14	4	1	19	7
Anatomy Systematics	1	1	0	1	3	1
Ageing Techniques	0	0	0	0	0	0
Methodology	1	0	0	0	1	0
Total	86	89	77	27	279	
Percent	31	32	27	10		

TABLE 2. Publications of the Fisheries Research Board of Canada in the 1960's that concerned Pacific salmon.

	Sockeye and Kokanee	Pink and Chum	Coho and Chinook	Pacific Salmon as a Group	Total	%
Life History Growth	12	26	8	15	61	13
Ecology Pollution	2	4	5	2	13	3
Behavior Migration	25	10	20	2	57	12
Parasites Diseases	7	12	11	7	37	8
Population Dynamics Management	27	29	19	16	91	19
Physiology	67	9	44	6	126	26
Enhancement	3	20	4	0	27	6
Anatomy Systematics	6	3	6	7	22	4
Ageing Techniques	4	10	1	0	15	3
Methodology	10	3	15	4	32	6
Total	163	126	133	59	481	
Percent	34	26	28	12		

TABLE 3. Publications of the Fisheries Research Board of Canada in the 1970's that concerned Pacific salmon.

	Sockeye and Kokanee	Pink and Chum	Coho and Chinook	Pacific Salmon as a Group	Total	%
Life History Growth	33	29	40	14	116	18
Ecology Pollution	16	11	33	13	73	11
Behavior Migration	17	8	22	3	50	8
Parasites Diseases	15	5	29	7	56	9
Population Dynamics Management	21	18	42	32	113	17
Physiology	20	9	77	9	115	18
Enhancement	23	23	23	13	82	13
Anatomy Systematics	2	5	2	3	12	2
Ageing Techniques	9	2	3	0	14	2
Methodology	3	3	7	3	16	2
Total	159	113	278	97	647	
Percent	25	17	43	15		

and a well deserved emphasis on that most famous of all the Pacific salmon, the sockeye.

The 1970's (Table 3) featured dramatic increases in the number of publications dealing with ecology and effects of pollution on salmonids, and enhancement techniques, together with a sustained effort on life history and growth, population dynamics and management, and physiology. The total number of publications on salmon went up to 647, an increase of 34% over the 1960's, but the relative interest in sockeye slipped to 25% in the 1970's, the decline being across the board and most noticeable in physiology. Those lesser species, coho and chinook, were most strongly emphasized in the 1970's — 43% of the total.

TABLE 4. Publications of the Fisheries Research Board of Canada in the period 1980–83 that concerned Pacific salmon.

	Sockeye and Kokanee	Pink and Chum	Coho and Chinook	Pacific Salmon as a Group	Total	%
Life History Growth	5	4	14	4	27	12
Ecology Pollution	2	0	3	3	8	4
Behavior Migration	1	4	15	1	21	10
Parasites Diseases	4	2	2	2	10	5
Population Dynamics Management	6	11	36	33	86	40
Physiology	2	2	5	0	9	4
Enhancement	4	17	12	11	44	20
Anatomy Systematics	1	0	0	1	2	1
Ageing Techniques	3	0	3	1	7	3
Methodology	0	0	0	2	2	1
Total	28	40	90	58	216	
Percent	13	18	42	27		

For the first 4 years of the 1980's population biology and management and enhancement were far and away the most dominant fields and the noble sockeye slipped to only 13% of the total as coho and chinook continued to be centre stage. Even the lowly pink and chum, accounting for 18%, outstripped the sockeye, the most famous of all of the Pacific salmon.

The total number of publications in the first 4 years of the 1980's (Table 4) was 216, which suggests that the decade might yield 540 publications, an ominous drop of 16% from the 1970's.

Looking back over the last 35 years, three things stand out as markers for what to do in the future. First, the conclusion can be drawn from the brief foray into publication statistics: *Do more research on sockeye*. This conference is obviously extremely timely. In one fell swoop the imbalance of the 1980's will be largely redressed so that sockeye will once more receive the attention they deserve. It is to be noted, though, that in this symposium there are no papers on physiology, and only scant attention to migratory behavior or systematics. Another symposium next year to patch up these deficiencies would probably be a good idea!

It might be added that more publications would help. It is my impression that the number of researchers is greater than it has ever been. The ratio of the biomass of salmon biologists to the biomass of salmon is now a measurable quantity, but the number of publications is falling off. There are probably many reasons for this and each of you will have his own theory. My excuse is that I am tired.

A second lesson for the future is that many of the shortcomings of our knowledge of 35 years ago are still shortcomings of our knowledge today. Though we know much more now about the marine migrations of sockeye, we are still fairly clueless about the marine ecology of sockeye in particular and Pacific salmon in general. The competitive relationships among the various stocks of sockeye, between sockeye and the lesser species of Pacific salmon, and between salmon and the even lesser species of the Pacific marine fish community are still obscure. Does the abundance of Bristol Bay sockeye influence the survival of Fraser sockeye? Does the abundance of pink, chum, coho, and chinook influence abundance of sockeye? Is the fishery for pollock in the Bering Sea a factor in the return of sockeye to Bristol Bay?

Even in fresh water where most attention has been directed, are we confident that we understand the factors influencing production of smolts? What are the dynamics of the relationship between sockeye juveniles and the other species of fish in the period of freshwater residence? Is the size of a cohort of sockeye substantially influenced by estuarial and near coastal conditions more than by conditions far at sea? And do we really know what optimum escapements should be?

We also know much more now about how sockeye *might* find their way home, but we still don't know how they *do* find their way home, nor why the path of their marine migration may vary from year to year such as by way of the Strait of Juan de Fuca or Johnstone Strait in southern British Columbia. I am increasingly convinced that we seriously underestimate the mental capabilities of fish in general and sockeye in particular. They may indeed be smarter than many of our researchers.

And so it goes, through the whole gamut of sockeye biology. Much is known but much remains to be discovered. I'm sure all of you can think of some major unanswered questions.

The third lesson to be learned is that research tends to follow both the trends of biology and the problems of the day, and it isn't that easy to sort out which of the two trends is being followed. In the 1960's, for example, physiology was very much in vogue as a discipline. The emphasis on sockeye physiology related in part to this trend but also in part to the need for better understanding of the temperature tolerances, and the respiratory constraints to swimming capabilities for fish confronted with hydroelectric dams. In the 1970's, the emphasis on behavior sprang from the fashion for doing ethology, a new "ology", and the stimulus from work on birds and bees on animal navigation. But this was also relevant to such questions as "What are the behavioral factors that influence the success of spawning and can the homing behavior be manipulated to advantage?" An example from the 1980's is the emphasis on genetics, which is much to the fore in science today and highly relevant both to managing salmon populations and aquaculture. Today, if someone says he has produced a sockeye that is eight feet long and has three fillets, you're not quite sure he is kidding.

Perhaps the lesson to be learned is that the growth of our knowledge of sockeye rests heavily on the general advance of scientific knowledge. Thirty-five years ago it would not have been possible to do electrophoretic studies of salmon stocks because the technique had not been developed. The experimental methodology of heritability studies was only in its infancy. Twenty-five years ago the word "ethology" had only recently been coined. I can remember hearing the word for the first time from Bill Hoar, who was always well up on the literature. It was about that time that the theories about imprinting and celestial navigation were being born. Only 15 years ago there was emerging evidence of magnetic detection in animals. (I recall Jim Mason playing around with the effects of magnetic fields on salmon under a hut at UBC in the early 1950's, but Jim was away ahead of his time and nothing came of it, unfortunately.) The developments in computing and applied mathematics have been critical to the sophistication of modelling over the past 30 years. There are many more examples, especially in such fields as limnology, oceanography, and ecosystem functioning. Consider how much more we think we know now than we thought we knew then.

If it is true that our knowledge of sockeye in particular and of fish and fisheries in general has depended in large part on advances elsewhere in science, it is evident that fisheries research agencies must cultivate basic research in their programs, for it is the basic researchers who, more than any others, are the pipelines to what is going on elsewhere.

If I had the opportunity tomorrow to start a whole new fisheries research institution, I'd hire a dozen young molecular biologists who would produce synthetic fish hormones, new vaccines for fish diseases, and who would learn how to use tissue culture and recombinant DNA techniques to genetically engineer strains of fish. I'd hire a dozen each of young specialists from such fields as population biology, resource management, behavior, migration, limnology, oceanography, and physiology, and throw in a few tame applied mathematicians, biochemists, and other assorted ancillary staff to keep as pets.

As an old fashioned ecologist, I'd be the boss and I'd tell them all to go to work on that most famous of all of the Pacific salmon, the sockeye, and to be prepared to present their findings for publication at symposia to be held at 3-year intervals.

And now, for those of you who would like to stick around afterward, I would be glad to present the technical appendix to my paper, which is entitled, "A mathematical model for predicting the number of publications concerning sockeye salmon for the next 100 years."

Congratulations on a fine and very timely symposium.

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